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Marine mortality of Atlantic salmon, *Salmo salar* L: methods and measures

Mortalité en mer du saumon atlantique, *Salmo salar* L. : détermination et mesures

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ABSTRACT

This publication contains the contributed papers to an international workshop on marine mortality of Atlantic salmon (*Salmo salar* L.) convened at the Department of Fisheries and Oceans, Gulf Fisheries Centre, Moncton, New Brunswick (Canada) from August 20-22, 2001. The Workshop was organised under an EU Concerted Action programme (SALMODEL) to facilitate a detailed review of the information on the survival of Atlantic salmon in the sea, methods to estimate natural mortality and the values currently used in modelling studies. The Workshop reviewed estimates of marine survival for salmon from a number of monitored rivers around the North East Atlantic and in North America, investigating the trends in marine mortality. While some common trends were evident, other contradictory indicators suggest that the migrations of salmon at sea and the factors contributing to mortality may be quite complex. The methods used to estimate mortality rates at sea are reviewed, and both the inverse-weight and the maturity schedule models indicate that M in the second year of sea life has probably been underestimated in the past. Finally the workshop considered factors operating in fresh water, estuarine (transitional) and marine environments that might influence survival at sea. Investigations have indicated some strong associations between growth at sea and survival. Growth can be mediated by several factors including temperature, food, competition (intra and inter-specific) and may influence subsequent vulnerability to predation. Associations between several of the factors and survival rates at sea may be indicative of possible causal mechanisms. Additionally, marine phase survival may be influenced by conditions experienced during the juveniles in freshwater and transitional phases of the life cycle or by factors which delay the entry of returning adults into their river of origin. Research to date has attempted to identify a dominant factor affecting mortality, but it is more likely that many factors are acting together and influencing survival. In the context of run-reconstruction modelling for the development of fisheries advice, it is concluded that mortality of salmon in the second year at sea is more likely to be in the order of 3% per month rather than the 1% per month previously used in ICES assessments.

RÉSUMÉ

Cette publication comprend les communications présentées lors d'un atelier international sur la mortalité en mer du saumon atlantique (*Salmo salar* L.) tenu au Centre des pêches du Golfe du Ministère des Pêches et des Océans, à Moncton au Nouveau-Brunswick (Canada), du 20 au 22 août 2001. Cet atelier a été organisé dans le cadre d'un programme d'action concertée de l'Union européenne (SALMODEL) pour faciliter un examen détaillé des données sur la survie en mer du saumon atlantique, des méthodes pour estimer la mortalité naturelle de celui-ci et des valeurs utilisées actuellement dans les études de modélisation. Les participants à l'atelier ont examiné les estimations de la survie en mer des saumons d'un certain nombre de rivières surveillées du nord-est de l'Atlantique et de l'Amérique du Nord afin d'étudier les tendances en ce qui a trait à la mortalité en mer. Certaines tendances communes sont évidentes, mais des indicateurs contradictoires suggèrent que les migrations en mer du saumon et les facteurs contribuant à sa mortalité pourraient être assez complexes. Ont également été examinées dans cet atelier les méthodes utilisées pour estimer les taux de mortalité en mer. Le modèle fondé sur la relation inverse entre le poids et la mortalité ainsi que celui fondé sur le calendrier de la maturité indiquent que la mortalité au cours de la deuxième année en mer a probablement été sous-estimée par le passé. Finalement, les participants ont examiné les facteurs liés aux milieux d'eau douce, estuariens (transitoires) et marins qui pourraient influer sur la survie en mer. Des analyses ont révélé certaines relations importantes entre la croissance et la survie en mer. Plusieurs facteurs peuvent influer sur la croissance, y compris la température, la nourriture et la compétition (intra- et interspécifique), et la croissance peut avoir un effet sur la vulnérabilité subséquente du saumon à la prédation. Les relations entre plusieurs de ces facteurs et les taux de survie en mer pourraient révéler l'existence de mécanismes causaux. Les conditions qui prévalent au cours du stade juvénile (en eau douce ou lors de la migration vers la mer) ou les facteurs qui retardent le retour des adultes dans leur rivière d'origine peuvent également avoir un effet sur la survie en mer. Les recherches menées à ce jour visaient à identifier un des principaux facteurs qui influent sur la mortalité, mais il semble plus probable que celle-ci dépend de nombreux facteurs qui interagissent entre eux. Dans le contexte de la modélisation de la reconstitution des stocks pour la formulation de conseils en matière de pêche, il a été conclu que la mortalité du saumon au cours de la deuxième année en mer a plus de chance d'être de l'ordre de 3 % par mois que de 1 % (valeur auparavant utilisée dans les évaluations du CIEM).

MARINE MORTALITY IN ATLANTIC SALMON (*Salmo salar* L.) – WHAT DO WE KNOW?

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BASIS FOR THE WORKSHOP

While the trends in indices of abundance (e.g. juveniles, smolts and adults) have varied between rivers and over time, the overall level of abundance of North Atlantic salmon (Salmo salar L.) stocks has declined steeply over the past two decades. Despite continuing efforts to reduce, and in many cases eliminate, fisheries, many stocks have shown little evidence of recovery. Even when all of the known potential freshwater impacts are taken into account, the stock dynamic models show a significant decline in overall survival, particularly for southern European and North American stocks. It is thus widely believed that there must have been significant changes in the factors affecting stocks while they are at sea. Understanding the factors that influence survival of salmon at different stages in the sea is therefore crucial to explaining the variability in recruitment of stocks to fisheries and allowing fishery managers to make informed decisions to protect and rebuild stocks. Even where these factors may be outside the direct control of managers, it is important that they understand them in order that they can take appropriate mitigating action.

The choice of backward-running (run-reconstruction) models rather than forward-running (life history) models to estimate pre-fishery abundance (PFA) of North Atlantic salmon (Rago et al. 1993; Potter et al. 1998) has been strongly influenced by the belief (or assumption) that natural mortality is high and variable in the post-smolt phase and lower after the first sea-year. Based upon an inverse-weight hypothesis model (Doubleday et al. 1979), the International Council for the Exploration of the Sea (ICES) had employed a value of 0.01 per month for the rate of natural mortality of salmon after the first sea-winter (e.g. ICES 2000). This estimate had not been reviewed since then, despite the widespread belief that the marine survival of most salmon stocks has declined in recent years. Such an assumption appears to be at odds with the concept of relating changes in PFA to changes in environmental factors, which must be assumed to operate in some way to affect survival.

SALMODEL, a European Union (EU) Concerted Action programme was set up to review approaches for assessing and managing Atlantic salmon stocks in the North East Atlantic. In the initial year of SALMODEL it became evident that reviews and modifications to the run-reconstruction and predictive models for salmon abundance were premised on assumed values of natural mortality of salmon at sea (M), particularly in the second year. SALMODEL considered that this issue could be best addressed in a special workshop in order to facilitate a detailed review of the information on the survival of salmon in the sea, methods to estimate natural mortality and the values currently used in modelling studies. A workshop was held from August 20-22, 2001 which was funded by the EU and hosted by the Dept. of

Fisheries and Oceans, Gulf Fisheries Centre, Moncton, NB, Canada. Participants from both sides of the Atlantic (see Appendix 1) met over two days to address questions associated with the estimation of M.

Apart from the SALMODEL workshop, factors which potentially contribute to variations in mortality of salmon at sea were also considered independently at two special workshops in North America, the first in Halifax (NS) in June 2000 (O'Neil et al. 2000; Cairns 2001) and a second meeting jointly sponsored by IBSFC, ICES, NASCO, NPAFC and PISCES in March 2002 in Vancouver (Canada) (NPAFC 2002). This illustrates the importance of this issue from both a scientific and management perspective and the difficulty in estimating marine mortality for various stocks and stock complexes.

In contrast to the other workshops, the objective of the SALMODEL meeting was to review estimation methods and measures of mortality for Atlantic salmon rather than address hypotheses related to factors which could condition or cause mortality. This information was urgently required for the revisions to the run-reconstruction and predictive models currently used by ICES to provide advice for international management of existing salmon fisheries.

Experts in salmon biology and assessment from Europe and North America were invited to attend the workshop and give presentations on specific topics relevant to the goal of reviewing and improving current estimates of M. These presentations have been edited and compiled to form the chapters of this report.

MARINE SURVIVAL ESTIMATES AND TRENDS

Chapter 1, presents a review of marine survival of Atlantic salmon in the NASCO North East Atlantic Commission (NEAC) area. The decline in many stocks in the NEAC area (ICES 2002) over the last decade has been attributed in part to low marine survival. For these analyses, 24 indices of one sea-winter (1SW) return rates and 19 indices of two sea-winter (2SW) return rates were available from five countries in the NEAC area. In more recent years, the NEAC area has been grouped into two distinct geographic regions (Northern and Southern Europe) for the purposes of assessments and development of PFA forecasting (ICES 2002). As the purpose of the review was to contribute to the development of inputs for predictive models for managing salmon stocks in the NEAC area, examination of combined indices of marine survival estimates representing the two geographic stock groupings were also examined. The highest mean survival rates were observed for wild salmon. Only half of the correlations between wild smolt and hatchery smolt survivals from the same rivers were significant indicating that inferring survival of wild stocks from hatchery survival indices should be subject to caution. The highest mean survivals were observed for the Southern European groups while the Northern European hatchery groups showed the lowest survival over time. However, there was a significant decline in marine survival for 1SW NEAC salmon over the period examined, although there was less evidence of consistent trends for 2SW salmon.

In chapters 2 and 3, marine survivals of Atlantic salmon from North America are reviewed. In chapter 2, time-series of smolt to adult returns ranging in length from 8 years to 30 years were examined for six rivers in the Newfoundland area of eastern Canada. Marine survival was highly variable and low, and in most cases the overall trend was decreasing. Neither the size of the smolts nor run-timing had consistent effects on survival among rivers, although these relationships were present in some rivers. As in the NEAC area, indices of survival appeared to be mainly random with little serial correlation. Trends in marine survival of hatchery raised Atlantic salmon from rivers in mainland Canada were reviewed in chapter 3, and similarities were observed in the declining trends in survival for one-sea-winter (1SW) and multi-sea-winter (MSW) salmon since 1987. While the decline in survival of wild smolts is known to have been somewhat alleviated by the closure of the commercial marine fisheries in large portions of eastern Canada in 1984, the survival of hatchery smolts declined significantly after 1985 and remains at a low level relative to historical values. Monitoring of the numbers of emigrating wild smolts and adult returns at the Morgan Falls fishway on the R. LaHave since 1996 indicated a significant correspondence between hatchery and wild smolt survival. Changes in wild smolt survival were not associated with their size or number. This analysis suggested that the survival of hatchery smolts in the marine environment, although offset to a considerable amount from wild smolt returns, was a reliable index of the relative performance of wild smolts.

METHODS FOR ESTIMATING M

In Chapter 4, a review of methods for estimating M (natural mortality) is presented. For salmon, there are numerous estimates of M for the juvenile freshwater stages because these life stages can be readily monitored and are not subjected to fisheries. Estimates of M during the marine phase are much more difficult to obtain because the adults enumerated back to the river have until recently been exposed to both natural and fishing mortality at sea. The quotient of returns to the river as either 1SW or 2SW salmon relative to smolt outputs is one of several direct methods for estimating sea survivals to the corresponding life stage. Marine survival for salmon is thus commonly expressed as the proportion of emigrating smolts that return to homewaters or to their river of origin as 1SW or 2SW adults (ICES 2000). Strictly speaking, these ratios are 'return rates' rather than survival rates and reflect the effects of both mortality and maturation. Changes in the age at maturation may affect the relative proportions of fish from the smolt year class returning as 1SW or 2SW salmon, but this may also be caused by changes in natural mortality in different areas of the ocean. Nevertheless, it has been convenient to consider these return rates as indicators of survival.

The presentation in Chapter 4 adds to the work of Ricker (1976) by additionally reviewing measures based on life history principles including longevity, mean age at maturity and inverse functions to weight. The inverse-weight method receives special consideration in Chapter 12 and the premise of this approach is reviewed in chapter 4. The method relies on the assumption that M decreases with body size because natural mortality was assumed to be primarily by predation. The parameters of the inverse-weight function have been derived using holistic approaches based on cross-species and cross-phyla analyses as well as species-specific estimates derived from observed weight and mortality measures. The inverse-weight analyses of Doubleday et al. (1979), which formed the basis of the M value used by ICES in the run-reconstruction of PFA in both the North American and NEAC models, is reviewed in some detail. An analysis using the same weight at age data as Doubleday et al. (1979) but assuming a linear growth function resulted in mortality rate estimates of between 0.01 and 0.02 per month, whereas analysis of recent size at age data from several North American rivers and one European river (R. Bush), resulted in monthly mortality values of up to 0.06.

A maturity schedule method is also presented and elaborated further in Chapter 5 which builds on the approaches described by Murphy (1952) and Ricker (1976). A similar approach termed "Murphy's Method" was used to estimate the ocean mortality of Icelandic ranched Atlantic salmon during the second year at sea by Jonasson et al. (1994) and an updated analysis of Icelandic stocks is presented in Chapter 6. The modified maturity schedule model allows for the estimation of survival rates during the first and second years at sea based on return of 1SW and 2SW salmon, known sex ratios, and output of smolts. The sensitivities of the maturity schedule method to input parameters, including sex ratio, and violations of the assumptions are reviewed. Estimates of mortality rates in the second year at sea as derived from the maturity schedule method for North American and Icelandic stocks were high. There were notable differences in the mortality rate estimates using the inverse-weight method compared to the maturity schedule method for some stocks and time periods. Both the inverse-weight and the maturity schedule models indicate that M in the second year of sea life is greater than 0.01 per month. The maturity schedule method results suggested that mortality in the second year at sea may also be driven by size-independent factors such as parasites, disease, temperatures, or even marine mammal predators which may not be constrained in their predation rates by the size range of salmon in the second year at sea.

FACTORS INFLUENCING M

Atlantic salmon occupy three aquatic habitats during their life cycle: freshwater, estuarine (transitional) and marine. The factors contributing to mortality are similar in all habitats (e.g., predation, competition, environmental) but are not independent. Freshwater conditions may impart a survival advantage (or penalty) to out-migrating smolts in certain years, and marine conditions may subsequently modify the spawning success in freshwater.

In freshwater, both density dependent and density-independent factors regulate abundance of Atlantic salmon (Elliott 2001). The response of juvenile salmon abundance to intra-specific competition is strongly compensatory and there is limited carrying capacity for juveniles within freshwater (Elliott 2001). In addition to the effects density may have on freshwater survival, disease susceptibility and transmission, predation, and displacement by adverse environmental conditions may vary with abundance of juveniles. The factors that are of interest in the context of marine survival are those which act in freshwater but which ultimately are expressed as variations in survival at sea.

Recent research presented in Chapter 7 has demonstrated that conditions within freshwater may be critical to the subsequent survival of Atlantic salmon at sea. High densities of juveniles can affect the growth and ultimately the size of the smolts that migrate to sea. As there is compelling evidence of size-dependent survival at sea in Atlantic salmon and other salmonids, it is clear that the conditions experienced in freshwater may modify survival in the ocean. Environmental conditions independent of abundance can also modify the energy reserves of juveniles and smolts as they go to sea, and their subsequent survival at sea.

Variations in environmental conditions may also affect the run-timing of smolts going to sea. Smolts transferred to seawater in which the temperature gradient from acclimation was greater than 4-6°C had poorer seawater challenge performance than those presented with a smaller temperature differential (Staurnes et al. 2001). As freshwater conditions in spring are more responsive to air temperatures and smolt migration has been shown to be cued to water temperatures (Thorpe 1988), a mismatch relative to marine conditions may occur.

There were no consistent patterns among rivers in survival relative to run-timing. For example, there was evidence from two Canadian rivers that cohort survival was lower either side of a central distribution of smolt run timing, suggesting the existence of a possible optimum window of opportunity, whereas this relationship was not present in three other rivers examined (Chapter 2). In Chapter 8, the examination of an index of smolt migration timing (date of the first smolt captured at the smolt trap at the bottom of the river), for the R. Bush (UK (Northern Ireland)) indicated that for several recent years when marine survival was particularly low the smolt run had started around two weeks earlier than had previously been observed. A significant linear relationship between marine survival and smolt migration date suggests that cohorts for which the run commenced earlier displayed poorer marine survival. In the case of the R. Bush, the average sea surface temperature taken from a coastal station 25 km north-west of the river mouth differed from river temperature by 2.4°C during the recent years of very poor marine survival, whereas, the differential was only 0.3°C during the previous three years, when marine survival was within the "normal" range. If recent abnormally early smolt runs on this river are being driven by climate change, then these effects may be expected on a wider group of rivers, and if persistent, could have long-term effects on stocks.

Freshwater contaminants may act in a number of ways to reduce marine survival. For example, poor growth at sea resulting from exposure to such chemicals could increase the mortality of salmon at sea. A review of the present state of knowledge on this issue is presented in Chapter 9. Exposure of juvenile salmon to sub-lethal concentrations of a range of freshwater contaminants such as pesticides and endocrine disrupting chemicals (EDCs) may operate to reduce survival in fish once they have migrated to sea (Madsen et al. 1997). Some pesticides are suspected of interfering with the parr-smolt transformation, and reduce the ability of the fish to physiologically adapt to saline conditions (Hoar 1988) and two such products have been examined recently. Previously in Atlantic Canada an insecticide used to control spruce budworm infestations contained high concentrations of a compound called 4 nonylphenol (4-NP) (Fairchild et al. 1999). From laboratory studies, these nonylphenols are known to be toxic to invertebrates and fish and to have estrogenic effects. Results from a study of Atlantic salmon populations in Canada suggested that declines in catch were related to exposure to water-borne 4-NP during parr-smolt transformation. The second product, atrazine, is a widely used pre-emergent herbicide often applied to corn crops. Recent laboratory studies have shown that Atlantic salmon smolts exposed to environmental levels of atrazine in freshwater, had reduced gill Na+K+ATPase activity and plasma ion concentrations. Subsequent exposure to seawater resulted in poor hypo-osmoregulatory performance and mortality. Moreover, there was a suggestion that modification of the physiological processes involved during smoltification by atrazine may also delay or inhibit smolt migration. In a subsequent study, it was found that relative to reference groups, there was a greater proportion of salmon exhibiting poor seawater growth in salmon smolt groups exposed to both atrazine and 4-NP (Moore et al. 2003). The response in all cases was bimodal, with growth effects occurring soon after treatments. Short-term exposure to acid water during the smolt migration has also been shown to impair the subsequent marine survival of Atlantic salmon (Staurnes et al. 1996).

There are numerous factors that affect survival of salmon in the marine environment, abiotic as well as biotic, and the interaction between them is poorly known. Several studies (Ricker 1976; Friedland et al. 1996) have indicated that post-smolt mortality may be growth mediated by mechanisms related to physiological processes and ocean climate. The decreased Atlantic salmon abundance in recent years has been most pronounced in North America, although there has also been a significant decrease in Europe, particularly the southern areas. The decline is more pronounced for MSW salmon than for 1SW salmon, suggesting that changes in the marine environment may differentially affect the survival of salmon in the sea. Friedland and Reddin (1993) showed that inter-annual variation in the area of potential post-smolt habitat at sea, defined as the area combining their optimal temperature and full marine salinity, was significantly correlated with catches of salmon from this area. Further studies described in Chapter 10, using time-series of smolt survival rates, seemed to confirm this. If the driving force behind marine mortality is temperature-related, one might predict that survival of salmon stocks migrating as post-smolts into the same area would be correlated. When this hypothesis was tested using time-series of survival estimates of wild salmon from two European rivers, the observations supported the hypothesis that most mortality takes place in the first year at sea. Furthermore, there were significant correlations in return rates between salmon from both rivers, suggesting that survival was driven by common marine factors.

Climatic variations play a major role in shaping the marine environment and can influence currents, gyres and sea surface temperature (SST). Such changes may impact upon salmon directly through altering factors influencing migration routes or indirectly by shifting the distribution, and/or quantity, of food availability at one or several levels in the oceanic food chain. Furthermore, sea temperature may also determine abundance and distribution of potential salmon predators and competitors. As water temperature declines, endothermic predators (marine mammals, seabirds) may have an advantage over cold-blooded (poikilothermic) salmon at sea. Temperature is also a key factor for the physiological metabolism of salmon, and thus affects growth rates, assimilation rates, and may subsequently modify the risks salmon take to feed and optimise growth rates. These interactions are discussed in Chapter 11. It is hypothesized that predation vulnerability could be exaggerated in periods of colder marine conditions if salmon cannot swim as fast and must spend more time in the upper water column assimilating prey as compared to periods when water temperatures are warmer and assimilation is more rapid.

Salmon grow relatively fast in the sea, but the plasticity of salmon growth makes the discrimination between the extent of genetic and environmental influences difficult. Mortality of salmon at sea and fish size have been hypothesised to be inversely related (Ricker 1976). Predation is probably the most important source of mortality, with fish that are in poor condition or diseased likely being eaten before they perish. Predation on smolts and post-smolts may be most severe in estuaries and fjords, just after the smolts have left freshwater. Small fish are exposed to a larger range of predator species than large fish and there are more predators inside the continental shelf than in oceanic areas (Cairns and Reddin 2000). In Chapter 12, the inverse-weight mortality assumption is used to model mortality using relative growth functions of Atlantic salmon at sea. This exploration suggests that mortality may also be important in the latter phase of salmon migration as they return to rivers to spawn.

In Chapter 13, two previous studies describing an approach for estimating exploitation rates using survival data post-fishery moratorium and the survival rates and behaviour of wild salmon grown in sea cages and released to spawn are summarized. The results highlight the importance of accounting for marine exploitation when examining trends in salmon survival and return data even when commercial fisheries have been closed. The sea-cage rearing experiment provides a unique characterization of critical periods of mortality of salmon in the marine environment.

Even at large sizes, Atlantic salmon are not immune to predation as they return to rivers for spawning. There are reports of adult salmon being predated upon by marine mammals in estuaries (Carter et al. 2001). If fish that are delayed are more likely to die than those moving upstream into the comparative safety of freshwater, then the overall natural mortality on the stock may be higher in years with low flows than in years with high flows. In chapter 14, the authors explore this question by examining the effect of variation in daily flows within a year, using a simple model in which flow variation is represented as the number of days above (high flow) or below (low flow) a threshold, which is estimated from the data. The model was applied to observed salmon counts on the R. North Esk, UK(Scotland) for the period 1988-97. Counts were lower during low flows, and higher in the days immediately following a switch to high flows. However, there was no clear evidence of any simple effect of the duration of the preceding sequence on the numbers moving upstream. It is therefore possible that once fish are delayed by more than a few days they are less likely to be stimulated to move upstream on increased flows. A second model, developed to test whether salmon are "lost" to a river because of low summer flows, did not support the hypothesis that fish delayed during the summer months are "lost" from the spawning escapement but needs to be applied to more data sets.

CONCLUSIONS

The factors that modify marine survival of Atlantic salmon remain elusive, but identifying and understanding them is crucial for explaining variability in recruitment and for the management of fisheries. Direct measures of mortality for the marine phase of the salmon life-cycle can be obtained for stocks returning at a single age at maturity, but for many populations, salmon return at two or more ages such that direct measures of mortality can only be obtained using models which take account of this life feature. Furthermore, the methods and data available for measuring marine mortality are limited to estimating the integrated mortality over a full year and do not provide a means to investigate changes within this period.

The greatest mortality of Atlantic salmon at sea occurs in the first year after smolt emigration, but mortality in both the first and subsequent years at sea can be highly variable. Many factors act together to influence the level of survival, although there are likely to be some dominant factors (e.g. the SST when the smolts emigrate to sea) that could be used in models to forecast PFA. The mix and contribution of individual factors is also likely to vary depending on, for example, the location, life stage, and genetic predisposition of different stocks/populations. In some instances, factors in the freshwater or transitional phases of the life cycle may have large effects on marine survival. However, freshwater conditions are less likely to have common influences on large numbers of stocks because conditions are likely to differ greatly between rivers and regions. Thus, it is unlikely that variation in freshwater conditions can be used in PFA forecast models at the scales required by ICES. One possible exception to this is climate change, which could influence stocks in a similar way over a wide area, through, for example, increasing river temperatures. This might lead to the use of both freshwater and marine environmental indices in predictive models.

RECOMMENDATIONS

The Workshop considered recommendations: to further investigate methods to estimate M; to review the value of M used in assessment models; to begin developing models to forecast PFA of North East Atlantic stocks; and to conduct experimental studies of factors affecting M during the marine phase.

The Workshop agreed that further investigation of the original Lorenzen (inverse weight) model was required, as this approach is derived at the species level by comparison across a large number of species and may not be fully applicable to elucidating M in individual stocks of one species. It was also felt that a modification of the inverse weight model should be considered, which would incorporate a length-based approach, reflecting the likelihood that swimming speed may be more directly related to mortality risk than weight. This is based on the theory that predator avoidance may be a critical factor influencing M. Alternative approaches to estimating variability in M should also be explored, for example utilising available data to examine growth trajectories through the first and second years at sea, on the premise that M is unlikely to remain constant at different growth rates. There are several North American and European datasets that will facilitate this. The Workshop also recommended that efforts be made to apply both the Murphy and inverse weight methods to European datasets (e.g. River Burrishoole and Bush data) to calculate M and investigate the apparent lower mortality rates in European than North American stocks.

Despite the need for further studies, the Workshop concluded that the basis for the value of M previously used in run-reconstruction models had been sufficiently questioned to recommend that ICES consider other estimates. It was clear that while M clearly varied across stocks and through time (both inter annually and a decreasing trend during the 1990s) there was reason to recommend that average values higher than 0.01 per month should be used (perhaps as much as 0.03 to 0.05 per month). This recommendation was adopted by ICES (2002) who have subsequently applied a value of 0.03 per month in salmon assessment models.

The Workshop recognised that there was sufficient evidence of the effects of marine conditions on North East Atlantic salmon stocks to start developing predictive PFA models along similar lines to that used to provide catch advice for North American stocks (ICES 2002). It was agreed that preliminary development of such models should centre on the use of marine environmental indices, such as SST in the spring, to determine if a relationship exists that may support prediction of future PFA for North East Atlantic stocks. This recommendation has been pursued in the subsequent work of the SALMODEL group.

The Workshop highlighted several areas of work on the factors affecting marine survival that required further investigation. In particular, it was noted that further work should be undertaken to assess the nature and extent of impacts of freshwater contaminants on subsequent survival of smolts at sea, particularly for Atlantic salmon. Experimental studies should also be carried out on mortality in the immediate post smolt phase, as 'failed smolt syndrome', often seen in salmon aquaculture, may also be involved in the declining survival of wild salmon. The model developed to test the hypothesis of additional mortality on 'delayed' adults should be tested with additional river datasets, where daily flow and adult return data are available. These studies may be appropriate for a European funded R&D project under a future framework programme.

Finally, the need to extend our knowledge of specific factors affecting the distribution of salmon at sea and the causes of natural mortality was highlighted throughout the Workshop and it is noted that NASCO has recently (2002) formed an International Co-operative Salmon Research Board which has specifically identified an urgent requirement to carry out research at sea to fill in substantial gaps in our knowledge of this phase of the salmons life-history. As any research at sea is expensive and time-consuming, this will require a high level of co-ordination on both sides of the Atlantic involving co-operation between international research agencies and combined use of existing resources.

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1

EXAMINATION OF MARINE SURVIVAL DATASETS FOR ATLANTIC SALMON (*Salmo salar* L.) IN THE NORTH EAST ATLANTIC AREA

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The data used in this review are from the report of the ICES Working Group on North Atlantic Salmon (2001) and should not be cited without permission of ICES and of the individuals and agencies involved in their collection.

INTRODUCTION

The current decline in many Atlantic salmon (*Salmo salar* L.) stocks in the North East Atlantic (ICES 2002) over the last decade has been attributed in part to low marine survival. While it may not be possible to identify any one specific cause of higher mortality in recent years, it would be important to know whether trends in marine survival are common to all stocks in the North East Atlantic or whether there is spatial variation in survival. Furthermore, the relationship between 1SW survival and 2SW survival could provide information on the differential survival rates of these stock for predictive modelling of regional and national stocks.

Tagging surveys that have been carried out in many countries for up to 20 years provide direct information on marine survival, the relative rate of return and exploitation rates for selected groups of fish. A comparative analysis of these data should indicate whether there are common marine survival trends between stocks from different locations in the North East Atlantic and between 1SW and 2SW stocks. The characteristics of some datasets presented annually to ICES (ICES 2001) are examined along with an analysis of the level of coherence between the time series with a view to developing inputs for predictive models for managing salmon stocks in the NEAC area.

METHOD

For these analyses, 24 indices of 1SW marine mortality and 19 indices of 2SW marine mortality were available from five countries in the NEAC area. The general locations are shown in Figures 1 and 2.

Summary information is given below and codes used in Tables 3 and 7 are shown:

Iceland

- Ellidar 1SW wild (ELLID1W)
- Vesturdalsa 1SW and 2SW wild (VEST1W and VEST2W)
- Midfjarda 1SW and 2SW wild (MID1W and MID2W)

- Midfjarda 1SW and 2SW hatchery (MID1H and MID2H)

Ireland

- Corrib 1SW and 2SW wild (CORR1W and CORR2W)
- Corrib 1SW and 2SW from hatchery smolts released upstream at Cong hatchery (CONG1H and CONG2H)
- Corrib 1SW and 2SW from hatchery smolts released downstream at Galway (GAL1H and GAL2H)
- Burrishoole 1SW wild (BURR1W), 1SW and 2SW hatchery (BURR1H), (BURR2H)
- Erne 1SW and 1SW hatchery (ERNE1H and ERNE2H)
- Shannon 1SW and 2SW hatchery (SHAN1H and SHAN2H)
- Screebe 1SW and 2SW hatchery (SCRE1H and SCRE2H)
- Lee 1SW and 2SW hatchery (LEE1H and LEE2H)
- Bunowen 1SW and 2SW hatchery (BUN1H and BUN2H)
- Delphi 1SW and 2SW hatchery (DEL1H and DEL2H)
- Burrishoole origin hatchery smolts released at Delphi (BURDEL1H and BURDEL2H)

France

- Nivelle 1SW wild (NIV1W)

UK (Northern Ireland)

- Bush 1SW wild and hatchery (BUSH1W and BUSH1H)

UK (Scotland)

- North Esk 1SW and 2SW wild (ESK1W and ESK2W)

Norway

- Imsa 1SW and 2SW wild and hatchery (IMSA1W, IMSA2W and IMSA1H, IMSA2H)

Drammen 1SW and 2SW hatchery (DRAM1H and DRAM2H)

Sweden

- Lagan 1SW and 2SW hatchery (LAGEN1H and LAGEN2H)

These time series of marine survival data are available in ICES (2001) and derive from tagging studies (coded wire tagging and Carlin tagging) or from direct extrapolation where full upstream and downstream counting facilities are available. Pearson correlation coefficients (r) were computed using SPSS®. Significance correlations are indicated at two levels, $p<0.05$ and $p<0.01$. Trends in marine survival were analysed using route regression (Rago, 1993). In these analyses, a significance level of $p<0.1$ was adopted following the convention in ICES (2002).

In more recent years, (ICES 2001) the North East Atlantic countries (NEAC) have been grouped into two distinct geographic regions for the purposes of assessments and development of pre-fishery abundance forecasting (ICES 2002). As the purpose of this review is ultimately to contribute to the development of inputs for predictive models for managing salmon stocks in the NEAC area, examination of combined indices of marine survival estimates representing the main geographic stock groupings were also examined. These groups were Northern Europe (i.e. Iceland, Norway, Sweden) and Southern Europe (i.e. Ireland, UK(Northern Ireland), UK(Scotland) and France). As mean marine survival values vary considerably in magnitude across locations, these values were initially standardised (z-scores) to allow pooling of the data. Standardised means for the eight main groups were also correlated i.e., Northern European wild and hatchery 1SW and 2SW salmon and Southern European wild and hatchery 1SW and 2SW salmon.

Summary information is given below and codes used in Tables 4 and 8 are shown:

Northern European

- 1SW and 2SW wild (ZNEW1SW and ZNEW2SW).
- 1SW and 2SW hatchery (ZNEH1SW and ZNEH2SW).

Southern European

- 1SW and 2SW wild (ZSEW1SW and ZSEW2SW)
- 1SW and 2SW hatchery (ZSEH1SW and ZSEH2SW).

RESULTS

1SW survival indices

Marine survival values for individual river 1SW returns are shown in Table 1 (wild) and Table 2 (hatchery). Of the 12 data sets available for wild salmon releases, only one (the Burrishoole) has an unbroken record extending back over 20 years. Five others have a continuous time series for at least 10 years, while the rest contain some breaks in the run over time or short continuous time series. Data for hatchery releases are more complete and of the 14 available data sets, three have continuous data for 19 years or more, seven have continuous data for over 10 years while the remainder are comprised of shorter time series or intermittent data over a long period. A number of time series represent minimum values or have not been corrected for tagging mortality while others have used assumed exploitation rates to derive total stocks sizes prior to homewater fisheries and thence marine survival.

Higher mean survival rates are shown for the wild tagged groups from the Corrib and Burrishoole (Ireland), Bush (N. Ireland) and the North Esk (Scotland). For hatchery fish, highest mean survival rates are shown for the Burrishoole and Delphi/Burrishoole origin (Ireland). A correlation matrix (Table 3) suggests some inter-correlation, with approximately 17% of all correlations (i.e. 46 of 276) being significant. Of the 46 significant correlations, 46% occur between the Irish indices. In particular, the Corrib wild index (CORR1W) shows significance in 39% of all possible correlations (9 of 23) and 64% of correlations with other Irish indices (7 of 11).

Correlations between wild and hatchery stocks released or tagged from the same rivers indicate that only half of these are significantly correlated with each other suggesting that inferring survival of wild stocks from hatchery survival indices should be carefully considered.

The mean survival values for the major geographic areas for 1SW salmon are shown in Figure 3. The highest mean survival is shown for the Southern European wild groups while the Northern European hatchery groups showed the lowest survival over time. However, there appears to be a broad similarity in the trends and route regression (Rago, 1993) of all indices combined, indicating a significant decline in marine survival for 1SW NEAC salmon over the period shown ($P < 0.1$).

Examination of the correlation matrix for the major geographic 1SW stock groupings (Table 4) again suggests some degree of inter-correlation between the Northern European wild and hatchery indices and between Southern European wild and hatchery indices. There was also a significant correlation between Southern European wild indices and Northern European hatchery indices. However, there was no correlation between survival indices for wild stocks from the Northern and Southern Europe. It is unclear, therefore, whether there are common factors influencing the marine survival of wild stocks originating from both of these areas.

2SW survival indices

Marine survival values for 2SW returns are shown in Table 5 (wild) and 6 (hatchery). Five indices of wild salmon survival are available of which only two have more than 15 years of data and there are gaps in the series. Two others have more than 10 years of data but again these are not consecutive. There are 14 indices of survival of 2SW hatchery salmon available. Of these, four contain at least 15 years of consecutive data, while four others have at least 10 years of data either consecutively or intermittently. The highest survival values for wild tagged salmon returning in their second year are shown for the North Esk (Scotland), while survival of hatchery released salmon is highest for the Lagan (Sweden) and Drammen (Norway).

The correlation matrix for 2SW survival data (Table 7) shows much less inter-correlation than the 1SW indices. Of the 171 possible correlations only 8% were significant, which is no more than expected by chance. None of the survival indices for wild and hatchery 2SW originating from the same river were significant. However, the data for 2SW survival is based on much lower numbers of fish returning and the result should be treated with caution.

Comparison of the mean 2SW indices (Fig. 4) by major geographic region again shows the highest overall survival for the Southern European wild fish. The lowest survival has consistently been shown for the Southern European hatchery fish. As with the 1SW fish, there is a tendency for a declining trend in marine survival of 2SW salmon and this is confirmed by route regression ($P < 0.1$, Rago 1993).

The major geographic regions were poorly correlated (Table 8) with only one significant correlation shown between Northern European wild and hatchery indices of survival.

Comparison of survival indices for 1SW and 2SW salmon

1SW survival and 2SW survival were poorly correlated (Table 9) even for the same release groups (e.g. Irish indices of survival for 1SW and 2SW derived from the same smolt groups released). Only the Imsa hatchery and wild 1SW and 2SW indices and the Drammen hatchery indices were significantly correlated. Both the Imsa wild and Drammen hatchery 2SW indices were correlated with a number of 1SW indices particularly from Ireland and UK (N. Ireland).

Grouping these indices by major geographic area (Table 10) indicated that Northern European wild and hatchery 2SW survival was only correlated with their corresponding 1SW hatchery survival. The survival of Southern European 2SW hatchery salmon was only correlated with its corresponding 1SW wild survival.

DISCUSSION

Although there was evidence of some inter-correlation between marine survival indices of several stocks originating from the Northern and Southern European areas, survival influences were not common to all stocks. Despite the distances between the rivers of origin, some inter-correlation would be expected as many of these stocks have been shown to occupy similar geographic areas at sea during the feeding phase of the migration particularly at Faroes (Jacobsen et al. 2000), and in the Norwegian Sea (Holst et al. 1993; Holst et al. 2000; Holm et al. 2000) and north of Scotland (Shelton et al. 1997).

Very little inter-correlation was shown between 2SW indices and between 2SW and 1SW indices, suggesting that the factors affecting mortality are not common to these groups, possibly because 2SW salmon may be much more widely dispersed than 1SW fish.

Despite the low level of inter-correlation, marine survival has been declining in both geographic regions and for both 1SW and 2SW stocks. While this does not imply a common cause for this decline, the importance of investigating specific marine factors is highlighted.

Representative indices for the Northern and Southern European stocks, or indeed other geographic groupings, could be developed but the lack of specific information on key causes of marine mortality in specific areas may limit the usefulness of these biological parameters for predictive modeling. However, these indices may be more useful when combined with physical oceanographic indicators of regime shift and oceanic variation over the same time period (e.g. North Atlantic Oscillation (NAO), regional changes in mean sea surface temperature (SST), Gulf Stream Indices (GSI) and indices of thermal habitat for salmon in the NEAC area).

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Table 1. Estimated marine survival rates for wild 1SW salmon from selected rivers in the North East Atlantic area (data from ICES 2001).

Smolt	Iceland			Ireland			UK (NI)	UK(Scot)	France		Norway
migration	Ellidaar	Vesturdalsa[4]	Midfjardara[4]	CombW[3]	BurnshooleW[6]	Moy	Bush[9]	N Esk	Nivelle[4]	Bresle	Imsa
year	1SW[1]	1SW[1]	1SW[1]	1SW[3]	1SW[1]	1SW	1SW[3]	1SW[2]	All ages[7]	All ages[7]	1SW[2]
1980				17.9	6.2						
1981				7.6	17.0			13.7			17.3
1982				20.9	17.5			12.6			5.3
1983		2		10.0	7.3						13.5
1984				26.2	26.0			10			12.1
1985	9.4			18.9	22.3			26.1			10.2
1986				-	22.7		31.3		15.1		3.8
1987			2.4	16.6	26.9		35.1	13.9	2.6		17.3
1988	12.7		0.6	14.6	28.4		36.2		2.4		13.3
1989	8.1	1.1	0.2	6.7	8.9		25	7.8	3.5		8.7
1990	5.4	1	1.2	5.0	18.9	10.7	34.7	7.3	1.8		3
1991	8.8	4.2	1.1	7.3	25.3	5.2	27.8	11.2	9.2		8.7
1992	9.6	2.4	1.4	7.3	16.5	8.1	29		8.9	6.9	6.7
1993	9.8		1	10.8	22.5	6.2			8.3	10.3	15.6
1994	9		1.4	9.8	29.7		27.1	17.2	7.2	7.5	
1995	9.4	1.6	0.3	8.4	14.0			11.5	2.3		1.8
1996	4.6	1.4	1.2	6.3	21.8		31	10.7	4.4		3.5
1997	5.3	0.7	2.4	12.7	17.9		19.8	10.3	3.3	4.87	1.5
1998	5.3	1	1.3	5.5	15.6		13.4		2		7.2
1999	7.7	1.3		4.6	20.3		16.5				3.7
Mean	8.1	1.7	1.2	11.4	19.3	7.6	27.2	12.7	5.5	8.2	8.5

[1] Microtags

[2] Carlin tags, not corrected for tagging mortality

[3] Microtags, corrected for tagging mortality

[4] Assumes 50% exploitation in rod fishery

[5] Minimum estimates

[6] From 0+ stage in autumn

[7] Incomplete returns in some years

[8] Assumes 30% exploitation in trap fishery

[9] Estimated from known exploitation rates from hatchery returns

Table 2. Estimated marine survival rates for hatchery 1SW salmon from selected rivers in the North East Atlantic area (data from ICES 2001).

Smolt	Iceland	UK (NI)	Norway		Sweden	Ireland									
migration	Midfjardara[4]	Bush[9]	Imsa	Drammen	Lagen	Burrishoole	Erne	Shannon	Comb US	Comb DS	Screebe	Bun(Delphi)	Delphi	Lee	Bunowen
year	1SW[1]	1SW[3]	1SW[2]	1SW[2]	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW
1980						4.7		8.6	0.9					10.8	
1981			10.1			9.1		2.8	1.2					2.0	
1982			4.2			9.9		4.1	2.7	16.1				16.3	
1983		1.9	1.6			3.3		3.9	1.7	4.1				0.0	
1984	0.5	13.3	3.8	3.5	11.8	26.9	9.2	4.9	5.2	13.2	10.4			2.1	
1985	0.4	15.4	5.8	3.4	11.8	32.1	7.9	17.4	1.4	14.4	12.3			15.7	
1986	0.4	2.0	4.7	6.1	7.9	9.8	10.1	16.4		7.6	0.4			16.3	
1987	2.7	6.5	9.8	1.7	8.4	16.1	6.9	3.1		2.2	8.3			8.6	
1988	0.7	4.9	9.5	0.5	4.3	17.1	2.6	4.9	4.2		9.2			5.5	
1989	0.7	8.1	3	1.9	5	10.1	1.1	5.0	6.0	4.9	1.8		0.2	1.7	
1990	1.9	5.6	2.8	0.3	5.2	10.9	1.3	1.3	0.2	2.3	-		0.5	2.5	
1991	1.8	5.4	3.2	0.1	3.6	13.9	1.3	3.8	3.5	4.0	0.3	10.8	1.8	0.8	
1992	1.3	6.0	3.8	0.4	1.5	7.5		4.3	0.9	0.6	1.3	10.0	6.1		5.2
1993	0.5	1.1	6.5	3	2.6	11.9		2.9	1.0		3.4	14.3	0.7		6.4
1994	1	1.6	6.2	1.2	4	13.7		5.1		5.3	1.9	5.6	1.4		8.1
1995	0.8	3.1	0.4	0.7	3.9	7.8		3.6	2.4		4.1	3.3	2.3		3.5
1996	0.1	2.0	2.1	0.3	3.5	5.7		2.9			1.8	9.9	8.9		3.3
1997	0.9		0.9	0.4	0.6	13.3	8.3	6.0			0.4	16.3	2.9	6.9	5.7
1998		2.3	2.4	1.9	1.6	4.9	2.5	3.1	3.3	2.9	1.3	7.1	4.7	4.6	2.6
1999		2.7	6	1.7	2.1	6.7	3.5	0.7		3.2	2.5	10.7	3.0		1.4
Mean	1.0	5.1	4.6	1.7	4.9	11.8	5.0	5.2	2.5	6.2	4.0	9.8	3.0	6.7	4.5

[1] Microtags

[2] Carlin tags, not corrected for tagging mortality

[3] Microtags, corrected for tagging mortality

[4] Assumes 50% exploitation in rod fishery

[5] Minimum estimates

[6] From 0+ stage in autumn

[7] Incomplete returns in some years

[8] Assumes 30% exploitation in trap fishery

[9] Estimated from known exploitation rates from hatchery returns

Table 3. Correlation coefficient matrix of 1SW marine survival for selected rivers in the North East Atlantic.

Correlations

		ELLID1W	VEST1W	MOY1W	CORRIB1W	BURR1W	BUSH1W	ESK1W	NIV1W	IMSA1W	MOY1H	BUSH1H	IMSA1H	DRAMM1H	LAGEN1H	BURR1H	ERNE1H	SHANN1H	CONG1H	GAL1H	SCRE1H	BUN1H	BURDEL1H	DEL1H	LEE1H
ELLID1W	r	1																							
	N	13																							
VEST1W	r	.582	1																						
	N	8	10																						
MOY1W	r	-.497	-.128	1																					
	N	11	8	12																					
CORRIB1W	r	.501	-.022	.437	1																				
	N	13	15	12	19																				
BURR1W	r	.253	.211	.353	.088	1																			
	N	13	15	12	19	20																			
BUSH1W	r	.404	.296	-.103	.424	.193	1																		
	N	10	8	10	11	12	12																		
ESK1W	r	.538	.479	.354	.343	.377	.033	1																	
	N	8	6	8	12	12	7	12																	
NIV1W	r	.329	.858**	.520	-.121	.255	.118	.440	1																
	N	11	8	12	12	13	11	8	13																
IMSA1W	r	.665*	.445	.079	.313	.093	.407	.326	-.025	1															
	N	12	10	11	17	18	11	11	12	18															
MOY1H	r	-.576	.459	.496	-.144	.142	.386	-.172	-.251	.231	1														
	N	11	7	11	13	14	10	10	12	13	14														
BUSH1H	r	.205	.166	-.527	.703**	.061	.335	.454	-.312	.235	-.015	1													
	N	12	9	11	15	16	11	9	12	15	13	18													
IMSA1H	r	.693**	.173	.169	.221	.538*	.462	.441	.088	.711**	.263	.122	1												
	N	13	10	12	18	19	12	12	13	18	14	16	19												
DRAMM1H	r	.187	-.444	-.075	.605*	.102	-.039	.500	.630*	.208	-.364	.187	.215	1											
	N	13	9	12	15	16	12	10	12	15	14	15	18	16											
LAGEN1H	r	.261	.087	-.018	.701**	.210	.672*	.482	.161	.306	-.060	.770**	.308	.561*	1										
	N	13	9	12	15	16	12	10	13	15	14	15	16	16	18										
BURR1H	r	.420	.249	.256	.620**	.471*	.547	.619*	-.021	.295	-.386	.847**	.307	.322	.790**	1									
	N	13	10	12	16	20	12	12	13	18	14	16	19	16	18	20									
ERNE1H	r	-.035	-.380	.861*	.843**	.246	.116	.408	.492	.049	-.359	.352	.100	.678*	.165	.307	1								
	N	8	8	7	10	11	9	7	8	11	9	10	11	11	11	11	11								
SHANN1H	r	.267	.091	.055	.509*	.047	.199	.820**	.720**	-.059	-.411	.415	.336	.601**	.574*	.491*	.634*	1							
	N	13	10	12	19	20	12	12	13	18	14	16	19	16	18	20	11	20							
CONG1H	r	.158	-.001	-.630	.204	.193	-.284	-.354	-.243	.036	-.524	.287	-.380	.167	.211	.255	.031	-.089	1						
	N	9	7	8	14	14	6	8	8	13	9	11	13	10	10	14	7	14	14						
GAL1H	r	.375	.043	-.458	.822**	.075	.015	.425	.164	.517	-.729*	.721**	.332	.644*	.830**	.615*	.686*	.504	.218	1					
	N	8	7	7	12	13	9	8	8	12	8	12	13	11	11	13	9	13	9	13					
SCRE1H	r	.568	-.285	-.035	.839**	.308	.558	.579	-.478	.660*	-.008	.741**	.519*	.215	.790**	.820**	.318	.276	.548	.709*	1				
	N	12	8	11	14	15	11	5	12	14	13	14	15	15	15	15	10	15	9	10	15				
BUN1H	r	.413	.162	.312	.768*	.062	.495	.814	.695	.468	.437	-.154	.305	.047	.155	.882**	.548	.749*	-.547	.380	-.119	1			
	N	8	6	7	8	8	6	4	7	7	8	7	8	8	8	8	3	8	4	4	8	8			
BURDEL1H	r	-.183	.029	.662	.547	.035	.135	-.487	.340	.334	-.039	.085	.089	.030	-.534	.452	.821	.283	-.444	-.448	-.450	.313	1		
	N	9	7	8	9	9	7	5	8	8	7	8	9	9	9	9	4	9	5	5	9	8	9		
DEL1H	r	-.297	.064	.251	-.179	.110	.124	.225	.123	-.301	-.402	-.262	.177	-.397	-.330	-.571	.381	-.026	-.256	-.641	-.156	-.207	-.098	1	
	N	11	9	10	11	11	9	7	10	10	9	10	11	11	11	11	8	11	7	7	10	8	9	11	
LEE1H	r	.352	-.655	.734	.500	.080	.180	.723*	.569	-.281	-.290	.169	.150	.613	.374	.189	.596	.738**	-.342	.564	.207	1.000**	[illegible]	.594	1
	N	7	6	7	15	14	6	8	9	13	9	10	13	10	10	14	10	14	11	10	9	2	3	5	14

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Table 4. Correlation matrix (z scores) for 1SW salmon from geographic areas.

Correlations

		ZNE1SW	ZNE1SH	ZSE1SW	ZSE1SH
ZNEW1SW	r	1			
	N	19			
ZNEH1SW	r	**.600****	1		
	N	**19**	19		
ZSEW1SW	r	.242	**.529***	1	
	N	19	**19**	20	
ZSEH1SW	r	.074	.293	**.810****	1
	N	19	19	**20**	20

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Table 5. Estimated marine survival rates for wild 2SW salmon selected rivers in the North East Atlantic area (data from ICES 2001).

Smolt migration year	Iceland		Ireland[1]	UK(Scot)	Norway
	Vesturdalsa[4]	Midfjardara[4]	CombW[3]	N.Esk	Imsa
	2SW[1]	2SW[1]	2SW[3]	2SW[2]	2SW[2]
1980			0.6		
1981			3.8	6.9	4
1982			3.3	5.4	1.2
1983			1.9		1.3
1984			2.0	4.1	1.8
1985			1.8	6.4	2.1
1986					4.2
1987		1.4	0.7	3.4	5.6
1988		0.9	0.7		1.1
1989	2	0.7	0.7	4.9	2.2
1990	1	1.3	0.6	3.1	1.3
1991	0.6	0.5	1.3	4.5	1.2
1992	0.8	0.5	0.0		0.9
1993		1.1	2.0		
1994		0.6	1.4	2.3	
1995	1.2	0.9	0.1	5.1	1.5
1996	0.3	0.7	1.2	3.5	0.9
1997	0.5	0.5	0.8	6.3	0.3
1998	1.04		1.1		1.1
Mean	0.93	0.83	1.33	4.66	1.92

[1] Microtags.

[2] Carlin tags, not corrected for tagging mortality.

[3] Microtags, corrected for tagging mortality.

[4] Assumes 50% exploitation in rod fishery.

[5] Minimum estimates.

[6] From 0+ stage in autumn.

[7] Incomplete returns.

[8] Assumes 30% exploitation in trap fishery.

Table 6. Estimated marine survival rates for hatchery 2SW salmon selected rivers in the North East Atlantic area (data from ICES 2001).

Smolt	Iceland	Norway		Sweden	Ireland[1]									
migration	Midfjardara[4]	Imsa	Drammen	Lagen	B'shoole	Erne	Shannon	Comb US	Comb DS	Screebe	Burr(Delphi)	Delphi	Lee	Bunowen
year	2SW[1]	2SW[2]	2SW[2]	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
1980							0.1	0.6					0.1	
1981		1.3						0.4						
1982		0.6						0.2	0.5				0.1	
1983	0.2	0.1						0.4	0.6					
1984	0.2	0.4	3.0	1.1	0.2	0.1	0.1	1.6	1.1	0.2			0.1	
1985	0.1	1.3	1.9	0.9	0.1	0.1		0.1	0.7	0.1				
1986	0.7	0.8	2.2	2.5	0.1	0.7			0.5				0.2	
1987	0.7	1.0	0.7	2.4	0.1				1.0	0.3			0.1	
1988	0.2	0.7	0.3	0.6	0.1	0.1	0.1	0.4		0.1				
1989	0.4	0.9	1.3	1.3	0.0			0.4	0.4				0.1	
1990	0.5	1.5	0.4	3.1	0.2	0.1	0.1	0.4	0.3	0.1		0.1		
1991	0.2	0.7	0.1	1.1	0.0	0.1	0.1	0.3	0.6		0.3	0.5		
1992	0.2	0.7	0.6	0.4	0.1		0.1	0.2	0.1	0.2	0.2	0.6		0.3
1993	0.2	0.5	1.0	0.9	0.1		0.1	0.3				0.4		0.3
1994	0.2	0.6	0.9	1.2	0.2		0.2		0.3	1.9	0.2			0.2
1995	0.1	0.0	0.3	0.6	0.2		0.1	0.3			0.2	0.2		0.1
1996		0.2	0.2	0.5	0.0		0.1			0.2	0.4	0.4		
1997		0.0	0.1	0.5	0.0						0.1	0.3	0.1	0.1
1998		0.1	0.6	0.9	0.0			0.2	0.1			0.1		
Mean	0.30	0.63	0.91	1.20	0.10	0.19	0.09	0.41	0.51	0.36	0.23	0.31	0.12	0.20

[1] Microtags.

[2] Carlin tags, not corrected for tagging mortality.

[3] Microtags, corrected for tagging mortality.

[4] Assumes 50% exploitation in rod fishery.

[5] Minimum estimates.

[6] From 0+ stage in autumn.

[7] Incomplete returns.

[8] Assumes 30% exploitation in trap fishery.

Table 7. Correlation coefficient matrix of 2SW marine survival for selected rivers in the North East Atlantic.

Correlations

		VEST2W	MID2W	CORR2W	ESK2W	IMSA2W	MID2H	IMSA2H	DRAM2H	LAGEN2H	BURR2H	ERNE2H	SHAN2H	CONG2H	GAL2H	SCRE2H	BURDEL2H	DEL2H	LEE2H	BUN2H
VEST2W	r	1																		
	N	8																		
MID2W	r	.278	1																	
	N	7	11																	
CORR2W	r	-.340	.022	1																
	N	8	11	18																
ESK2W	r	.097	-.400	.444	1															
	N	6	8	12	12															
IMSA2W	r	.877**	.688*	.241	-.043	1														
	N	8	9	15	11	16														
MID2H	r	.372	.675*	-.282	-.476	.802**	1													
	N	5	9	12	8	11	13													
IMSA2H	r	.330	.512	.193	.033	.493	.456	1												
	N	8	11	17	12	16	13	18												
DRAM2H	r	.877**	.194	.595*	.090	.397	.111	.228	1											
	N	8	11	14	10	13	12	15	15											
LAGEN2H	r	.285	.723*	-.047	-.515	.640*	.861**	.661**	.223	1										
	N	8	11	14	10	13	12	15	15	15										
BURR2H	r	.171	.457	.004	-.402	.186	-.128	.246	.335	.317	1									
	N	8	11	14	10	13	12	15	15	15	15									
ERNE2H	r	.[a]	.[a]	.619	.012	.944**	.811	-.118	.358	.464	-.108	1								
	N	2	3	5	4	6	6	6	6	6	6	6								
SHAN2H	r	-.496	-.296	.204	-.712	-.066	-.087	.010	.060	.066	.350	1.000**	1							
	N	5	8	10	6	7	8	9	9	9	9	4	10							
CONG2H	r	.552	.526	.089	-.389	.126	.059	-.144	.710*	.107	.447	.219	-.180	1						
	N	6	7	14	8	12	10	13	10	10	10	5	8	14						
GAL2H	r	.044	.545	.358	.171	.512	.105	.072	.543	.183	.237	-.264	-.258	.711*	1					
	N	5	6	11	8	11	10	12	10	10	10	5	5	9	12					
SCRE2H	r	-.721	-.378	.195	-.561	.662	-.140	-.227	-.038	-.022	.402	.333	.998**	.542	-.291	1				
	N	3	6	8	6	7	7	8	8	8	8	4	6	5	6	8				
BURDEL2H	r	-.423	.201	.408	-.500	.384	.333	.210	-.201	.094	-.328	.[a]	-.375	.500	.918	-.500	1			
	N	5	6	6	5	5	4	6	6	6	6	1	5	3	3	3	6			
DEL2H	r	-.553	-.702	.062	.148	-.294	-.493	.011	.019	-.512	-.308	.[a]	.047	-.352	.228	.918	.277	1		
	N	7	7	8	5	7	5	8	8	8	8	2	6	6	4	3	5	8		
LEE2H	r	.[a]	.[a]	.248	-.231	.408	.544	.242	.357	.608	.134	1.000**	.[a]	.322	-.345	.[a]	.[a]	.[a]	1	
	N	2	3	6	5	6	4	6	5	5	5	2	2	4	5	2	1	1	7	
BUN2H	r	-.082	.186	.322	-.956	.000	.870	.892*	.782	.153	.000	.[a]	-.174	-.500	-1.000**	-1.000**	.522	.845	.[a]	1
	N	3	5	5	3	3	4	5	5	5	5	0	4	3	2	2	4	4	1	5

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

[a] Cannot be computed because at least one of the variables is constant.

Table 8. Correlation matrix (z scores) for 2SW salmon from geographic areas.

Correlations

		ZNE2SW	ZNE2SH	ZSE2SW	ZSE2SH
ZNE2SW	r	1			
	N	18			
ZNE2SH	r	**.782****	1		
	N	**18**	18		
ZSE2SW	r	.187	.218	1	
	N	17	17	18	
ZSE2SH	r	.294	.391	-.110	1
	N	18	18	18	19

**. Correlation is significant at the 0.01 level (2-tailed).

Table 9. Correlation coefficient matrix of 2SW vs 1SW marine survival for selected rivers in the North East Atlantic.

Correlations

		VEST2W	MID2W	CORR2W	ESK2W	IMSA2W	MID2H	IMSA2H	DRAM2H	LAGEN2H	BURR2H	ERNE2H	SHAN2H	CONG2H	GAL2H	SCRE2H	BUN2H	BURDEL2H	DEL2H	LEE2H
ELLID1W	r	.375	.024	-.005	.170	.327	**-.689***	.207	.261	-.284	.352	.061	.053	.083	.416	.067	.625	-.250	.523	a
	N	8	10	12	8	10	9	12	12	12	12	4	8	9	7	8	5	6	8	2
VEST1W	r	-.253	-.424	.185	-.109	.041	-.518	.113	-.286	-.148	-.108	a	.318	-.194	.500	.721	.849	.356	.680	a
	N	8	7	9	6	9	6	9	8	8	8	2	5	7	6	3	3	5	7	2
MID1W	r	**-.722***	.077	.086	-.043	.286	.589	-.023	-.242	.206	-.140	a	.390	-.589	.483	.123	-.098	-.430	.111	a
	N	8	11	12	8	10	9	12	12	12	12	3	8	8	7	6	5	6	8	3
CORR1W	r	-.286	.309	.284	.155	.176	-.086	.018	**.739****	-.037	.336	.746	-.084	**.661***	**.774****	-.164	-.357	**-.837***	.242	.087
	N	8	11	18	12	15	12	17	14	14	14	5	10	14	11	8	5	6	8	6
BURR1W	r	**-.849****	.159	.083	-.524	.247	.094	.221	.149	.133	.308	-.182	.426	.188	.387	.520	.286	.308	.469	.257
	N	8	11	18	12	16	13	18	15	15	15	6	10	14	12	8	5	6	8	7
BUSH1W	r	-.120	**.745***	-.267	-.732	.394	.374	**.687***	.062	.426	.545	-.214	-.506	.642	.568	-.690	.947	.830	.314	.345
	N	7	9	10	7	10	8	11	11	11	11	4	6	6	8	6	3	5	6	4
ESK1W	r	-.558	-.109	.268	.255	.250	-.387	.272	.287	-.214	.128	.193	**.886***	-.353	.129	.192	.987	-.159	.657	.794
	N	6	8	12	12	11	8	12	10	10	10	4	6	8	8	6	3	5	5	5
NIV1W	r	-.326	-.502	.375	-.190	.262	.147	.114	**.627***	.118	-.005	.846	.208	-.408	.012	.469	**.965****	.192	**.911****	**.998****
	N	8	11	12	8	11	10	13	13	13	13	4	8	8	8	6	6	6	8	4
IMSA1W	r	.371	.452	.430	.108	**.539***	-.037	.303	.271	.042	.068	-.541	-.352	.236	**.699***	.403	.834	.370	.372	-.362
	N	8	10	16	11	16	12	17	14	14	14	6	8	13	11	7	4	5	8	6
MID1H	r	.001	.438	-.387	-.356	.370	.444	.404	-.377	.509	.098	-.381	.027	-.233	.068	.015	.086	-.298	-.098	-.378
	N	7	11	13	10	12	12	14	14	14	14	6	9	9	9	8	5	6	7	5
BUSH1H	r	.613	.062	.164	.637	.092	-.163	.487	**.566***	-.011	.132	-.533	-.322	.404	.545	-.449	.166	-.205	.242	-.783
	N	7	10	14	9	13	13	15	14	14	14	6	9	11	11	8	4	5	7	4
IMSA1H	r	.121	.463	.352	.038	**.660****	.280	**.582***	.162	.228	.190	-.053	.267	-.021	.449	.119	.787	.088	.417	.050
	N	8	11	17	12	16	13	18	15	15	15	6	9	13	12	8	5	6	8	6
DRAMN1H	r	**.731***	.402	**.700****	.236	**.582***	.350	.172	**.845****	.329	.148	.767	.026	.391	.353	-.057	.528	-.367	-.166	.864
	N	8	11	14	10	13	12	15	15	15	15	6	9	10	10	8	5	6	8	5
LAGEN1H	r	.506	**.714***	.448	.053	**.569***	.194	.498	**.787****	.388	.404	.062	-.062	.556	**.840****	-.236	-.067	.580	-.274	.155
	N	8	11	14	10	13	12	15	15	15	15	6	9	10	10	8	5	6	8	5
BURR1H	r	-.042	.253	.139	.145	.145	-.194	.372	**.583***	.010	.298	-.466	.090	.340	**.645***	-.139	-.132	-.444	.220	-.195
	N	8	11	18	12	16	13	18	15	15	15	6	10	14	12	8	5	6	8	7
ERNE1H	r	-.512	.044	.524	.386	.403	.194	-.150	.625	.021	.311	.560	.407	.579	.660	.505	a	**-1.000****	.152	.470
	N	5	6	9	7	10	8	10	10	10	10	6	4	7	8	5	1	2	4	5
SHAN1H	r	.108	**-.690***	.010	.425	.249	.110	.233	**.573***	.099	.002	.584	.157	-.099	.165	-.075	-.496	**-.871***	.435	**.925****
	N	8	11	18	12	16	13	18	15	15	15	6	10	14	12	8	5	6	8	7
CONG1H	r	.650	-.442	-.052	-.175	-.046	.045	-.289	.331	-.235	-.353	.714	.032	.409	.376	.283	**-1.000***	.828	-.041	-.660
	N	6	7	14	8	12	10	13	10	10	10	5	8	14	9	5	3	3	6	4
GAL1H	r	.561	-.304	**.841****	.677	-.065	-.333	.028	**.840****	-.183	.258	-.070	.027	.268	.443	-.120	**-1.000****	.258	-.259	-.113
	N	5	6	11	8	11	10	12	10	10	10	5	5	9	12	6	2	3	4	5
SCRE1H	r	.394	**.790****	.323	.162	.259	-.185	.439	.443	.049	.454	-.595	-.235	.398	**.743***	-.467	.041	.037	-.272	-.451
	N	7	10	13	9	12	11	14	14	14	14	5	8	9	9	7	5	6	7	5
BUN1H	r	-.301	-.111	.364	-.387	-.687	.790	.632	.564	.483	.479	a	.769	.364	.880	.915	.364	-.509	.571	a
	N	5	6	7	4	5	4	7	7	7	7	0	5	4	3	3	5	5	6	1
BURDEL1H	r	-.785	-.114	.363	.489	**-.900***	.745	.132	-.121	-.206	-.558	a	-.377	.145	.448	**-1.000***	.242	-.167	.447	a
	N	6	7	8	5	6	5	8	8	8	8	1	6	5	4	3	5	6	7	1
DEL1H	r	-.630	-.408	-.152	-.183	-.481	-.509	-.398	-.390	-.540	-.254	a	-.114	**-.863***	-.639	-.310	.255	.627	.409	a
	N	8	9	10	7	8	7	10	10	10	10	2	7	7	6	4	5	6	8	2
LEE1H	r	-.407	.379	.134	.343	.223	.261	.163	.279	.121	.034	.570	.290	-.428	-.001	-.136	a	**-1.000****	-.350	.525
	N	5	6	13	9	13	9	13	10	10	10	6	5	11	10	5	1	2	4	7

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

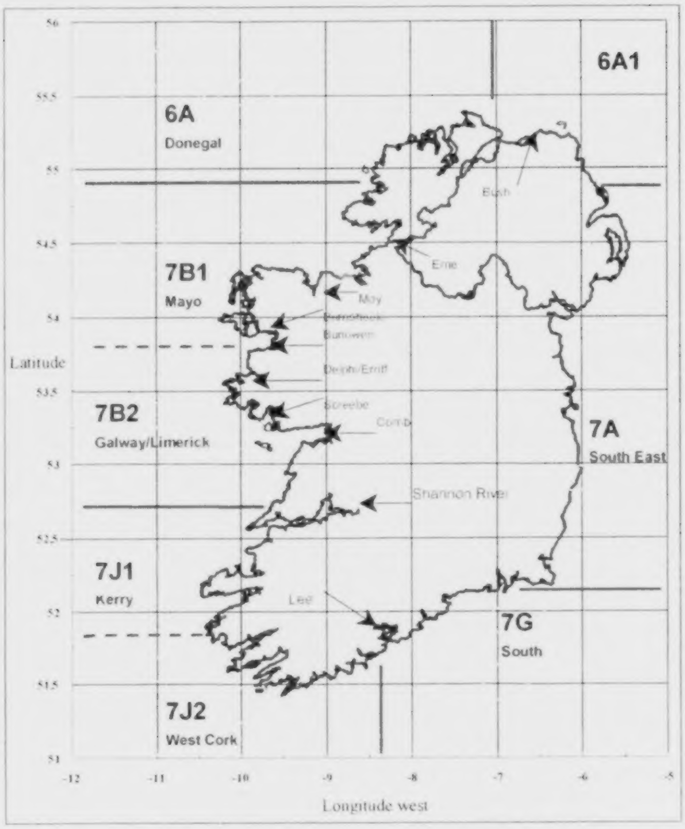
a Cannot be computed because at least one of the variables is constant.

Table 10. Correlation matrix (z scores) for 2SW vs 1SW salmon from geographic areas.

Correlations

		ZNE2SW	ZNE2SH	ZSE2SW	ZSE2SH
ZNE1SW	r	.345	.254	.251	.241
	N	18	18	17	18
ZNE1SH	r	**.760****	**.848****	.362	.380
	N	**18**	**18**	17	18
ZSE1SW	r	.215	.374	.120	**.598****
	N	18	18	18	**19**
ZSE1SH	r	.015	.145	.205	.229
	N	18	18	18	19

**. Correlation is significant at the 0.01 level (2-tailed).


56
55.5
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51.5
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Latitude
-12
-11
-10
-9
-8
-7
-6
-5
Longitude west
6A1
6A
Donegal
Bush
Erne
7B1
Mayo
Moy
Bunowen
Delphi/Erriff
Screebe
Corrib
7B2
Galway/Limerick
7A
South East
Shannon River
7J1
Kerry
Lee
7G
South
7J2
West Cork

Figure 1. River mouth locations of Irish rivers with indices of marine survival.

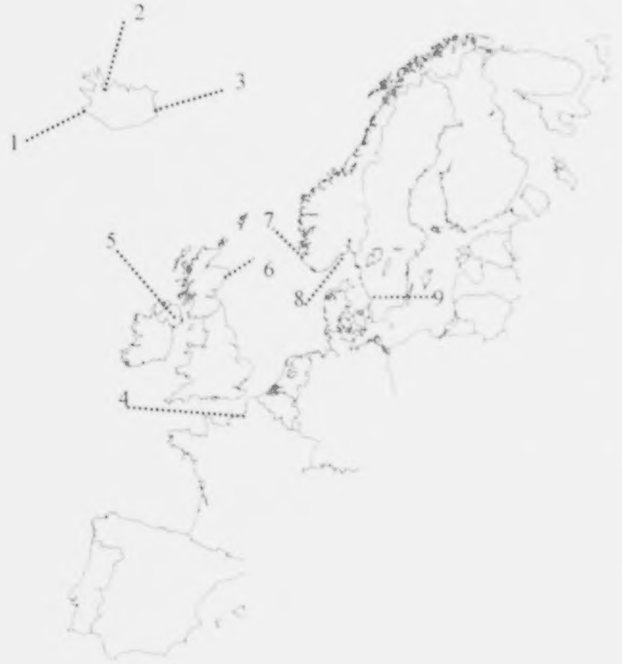

Figure 2. Other rivers and locations where marine survival indices have been derived. Number indices refer to the following: 1- Ellidar (Iceland), 2 – Midfjarda (Iceland), 3- Vesturdalsa (Iceland), 4- Nivelle (France), 5 - Bush (UK N. Ireland), 6 - North Esk (UK Scotland), 7 – Imsa (Norway), 8 - Drammen (Norway), 9 - Lagan (Sweden)

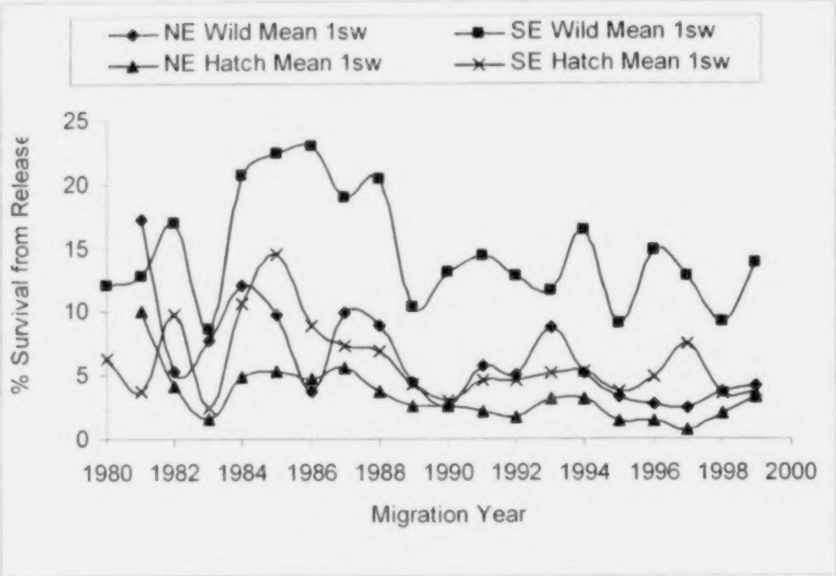

Figure 3. Comparison of 1SW marine survival for four main groups, Northern European (NE) wild and hatchery, and Southern European (SE) wild and hatchery.

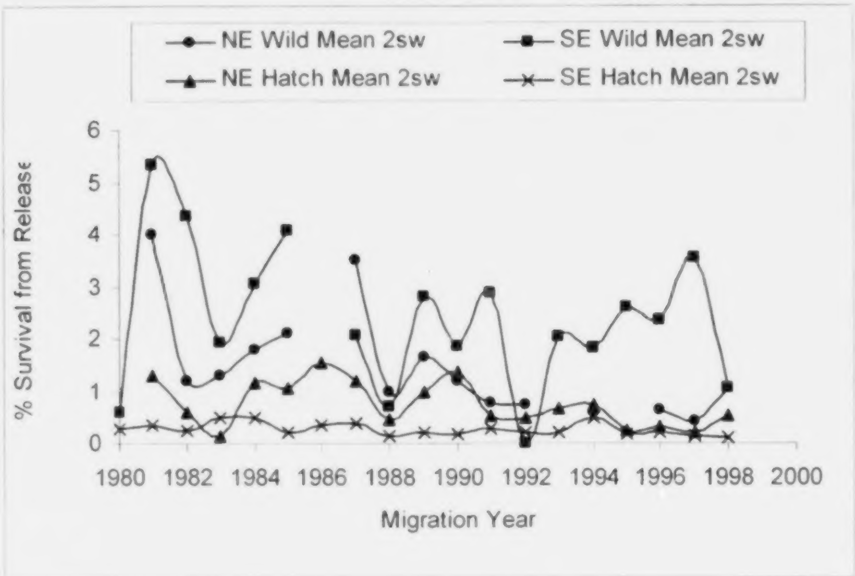

Figure 4. Comparison of 2SW marine survival for four main groups, Northern European (NE) wild and hatchery, and Southern European (SE) wild and hatchery.

2

PERSPECTIVES ON SMOLT PRODUCTION AND MARINE SURVIVAL OF NEWFOUNDLAND ATLANTIC SALMON (*Salmo salar* L.) RELATED TO SMOLT SIZE AND RUN TIMING

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INTRODUCTION

Counts of Atlantic salmon (*Salmo salar* L.) smolts and adult small salmon (salmon< 63 cm) enable estimates of marine survival to be derived. Examination of survival trends over time can provide insight into the effects of management measures designed to reduce marine exploitation, or, in the absence of fisheries allow estimates of natural survival to be calculated. Counts of smolts also provide a direct measure of freshwater production, and in some cases, allow estimates of egg-to-smolt survival to be obtained and evaluated in relation to current conservation requirements.

Many factors act to influence the survival and production of Atlantic salmon (Saunders 1981; Dempson et al. 1998; McCormick et al. 1998; Parrish et al. 1998; Armstrong et al. 1998). Consequently, survival, and hence adult salmon abundance, is often highly variable, both in Atlantic (Chadwick 1988; Dempson et al. 1998) and in Pacific salmon populations (Noakes et al. 1990; Hargreaves 1994). Some factors, such as run timing and smolt size, have been shown to have a more consistent influence on the subsequent survival to the adult life stage (e.g. Ward and Slaney 1988; Hansen and Jonsson 1989, 1991; Ritter 1989; McCormick et al. 1998; Salminen et al. 1995; Finstad and Jonsson 2001). In contrast, Hargreaves (1994) stated that many attempts have been made to relate marine survival rates to environmental parameters, and while observed patterns have often assisted in forecasting subsequent salmon abundance, frequently the resulting relationships showed little consistency among stocks, and among years within a stock.

In this paper we provide a summary of the variation in Atlantic salmon smolt production and marine survival from six Newfoundland rivers. Results are discussed in the context of variation in smolt run timing and smolt size on subsequent marine survival.

METHODS

Information on smolts and adult salmon counts is available from six rivers in Newfoundland (O'Connell et al. 2001): Campbellton River (Salmon Fishing Area (SFA) 4); Northeast Brook, Trepassey (SFA 9); Rocky River (SFA 9); Conne River (SFA 11); Highlands River (SFA 13); and Western Arm Brook (SFA 14A). While the time series of data vary in length among rivers, each of the above has information that allows direct comparisons back to the 1993 smolt class through to 2000. Smolt counts at Highlands River were discontinued following the 2000 season. In the following discussions, information on marine survival back to the river pertains to returns of small salmon only, and values have not been adjusted or corrected for marine exploitation in years prior to 1992. Small salmon are predominantly maiden one-sea-winter (1SW) fish, but could also include some repeat spawners and possibly some 2SW salmon.

Besides individual survival values for each river, a composite index of survival for all rivers was created. In this case the number of smolts and subsequent adult small salmon were added by year across each of the six rivers. Thus, the composite index is weighted by the respective numbers of fish from each river. The composite survival values were then standardized by subtracting the overall mean value from each year and dividing by the standard deviation.

Smolt run timing corresponded to the 50th percentile (median) day-of-the-year when smolts migrated.

Simple correlation analyses (Spearmans rank correlation, Sokal and Rohlf 1998) were used to measure the covariation among rivers of the following variables: smolt production, smolt survival, and run timing. In each case, correlation analyses were carried out on values that were standardized in the manner described above.

RESULTS AND DISCUSSION

Smolt Production

Table 1 summarizes the time series of data available on smolt production and marine survival. The longest continuous series pertains to Western Arm Brook, SFA 14 (1971 – 2001), the shortest series are from Campbellton River (SFA 4) and Highlands River (SFA 13) (1993 – 2001). Data for 2001 are considered preliminary.

Smolt production varies among rivers, and among years within rivers (Fig. 1). Variation within rivers, however, is relatively low with coefficients of variation ranging from 18.1% (Conne River) to 34.0% (Rocky River). Peak smolt runs occurred in 1997 in four of the six monitored rivers (Fig. 1), but declined successively in each of the following three years. Preliminary information from 2001 suggests smolt runs increased in four of five rivers; in contrast a substantive decline in smolt production occurred at Northeast Brook, Trepassey (Fig. 1). Note that smolts were not monitored at Highlands River in 2001. Table 2 summarizes Spearman correlation coefficients illustrating the degree of correspondence in smolt production among rivers. With few exceptions (e.g. Conne River with Rocky, Western Arm Brook and Campbellton rivers), annual variation in smolt production among rivers is not strongly coherent.

Marine Survival

Marine survival similarly varies among rivers, and among years within rivers (Table 1, Fig. 2). Variability in annual survival is greater than, say, variation in smolt numbers themselves; coefficients of variation exceed 35% in four of six rivers and is greater than 45% in three rivers. Part of the variation may be due to differential exploitation affecting some stocks prior to the closure of the commercial fishery in 1992.

Over all years for which data are available mean survival has ranged from a low of 1.6 % at Highlands River to a high of 6.0% at Campbellton River (Table 1). For all rivers combined since 1984, there are a total of 73 individual survival estimates. In general, survival rates are log-normally distributed with the most common values falling between 2 to 4%. Only 11% of the survival values recorded since 1984 exceed 8% despite the closure of the commercial Atlantic salmon fishery beginning with adult salmon returns in 1992. Several rivers have experienced marine survival rates that are lower, on average, than values prior to the closure of the commercial salmon fishery (e.g. Northeast Brook, Trepassey and Conne River). Marine survival of salmon to Western Arm Brook was substantially higher during the moratorium years of 1992 to 2001 by comparison with that experienced during the 1984 salmon management plan years up to and including returns in 1991. However, marine survival for the period 1972 to 1983 is not statistically different from that experienced during the moratorium (1992 – 2001) (nonparametric

Wilcoxon 2-sample test: Z = 0.990; P = 0.32) yet in the former period commercial fisheries were operating.

Figure 3 illustrates a composite index of standardized survival for all rivers combined. Collectively, negative survival anomalies occur at greater frequency than positive anomalies, with four of the past five years characterized by negative survival anomalies. At times, years with moderately large positive survival anomalies are followed by moderately large negative anomalies as observed in Figure 3 for returns in 1990 to 1991, 1996 to 1997, and 2000 to 2001. This figure also illustrates the overall lack of consistent response, in terms of increased marine survival, resulting from the closure of the commercial Atlantic salmon fishery. This was somewhat unexpected given that estimates of the median marine exploitation rate during the period from 1984 to 1991 were 45.3% (29.6 - 57.1%) on small salmon to 74.2% (57.7 – 83.7%) on large salmon (Dempson et al. 2001b).

Table 3 summarizes correlation coefficients illustrating the correspondence in smolt survival among rivers. Patterns of survival appear to be random and not serially correlated among rivers.

Smolt production and subsequent adult salmon

The relatively high variability in marine survival among and within rivers influences the subsequent pattern of adult salmon returns. In general, the emigration of greater numbers of smolts from a river does not consistently result in more adults returning in the following year as illustrated in Figure 4. Thus the high variation in marine survival often precludes accurate predictions of subsequent adult salmon abundance.

Association of run timing with marine survival

Run timing of smolts can vary substantially among years. For example, at Conne River, the median date of smolt migration can vary by as much as 22 days from one year to another (Dempson et al. 2001a). During the period 1987 to 1995 there was an apparent association between marine survival and timing of the out migration of smolts (Fig. 5) although the functional basis for this was unknown and probably non-existent. Run timing in 1996 was the earliest recorded followed by the latest run in 1997. However, the resultant marine survival was low in both cases and subsequent years provide speculative results showing that perhaps smolt runs can be either too early or too late in the context of the appropriate "smolt window" (Power and Power 1987; Hansen and Jonsson 1989; McCormick et al. 1998) for optimal survival. We note that Ritter (1989) has also reported a parabolic relationship between recapture rates and smolt release time. When other rivers are examined, Campbellton River has a suggestion of some similarity with Conne River in that lower marine survival could occur from either early or late smolt migrations (Fig. 6). However, collectively there is no apparent association simply between time of smolt migration and subsequent marine survival (Fig. 6) and it is likely that other, perhaps confounding factors, can mask any consistent relationship from being apparent.

In contrast with results from either smolt production or marine survival, there is a high degree of congruence in smolt run timing among rivers (Table 4). This suggests that although run timing differs among rivers, the pattern of early versus late runs is likely influenced to a large degree by environmental conditions affecting much of Newfoundland during the spring.

Association of smolt size with marine survival

It is commonly believed that smolt to adult survival is affected by the size of out-migrating smolts (e.g. Ward and Slaney 1988; Holtby et al. 1990; Salminen et al. 1995). A plot of mean smolt length or weight against average marine survival during the commercial salmon fishery moratorium years (1992 – 2001) suggests similar relationships may exist among Newfoundland salmon stocks (Fig. 7). Although marine survival of Rocky River smolt is anomalously low given the size of smolts, there is a general tendency for stocks with larger smolts to have, on average, correspondingly higher survivals (Fig. 7).

Within a stock survival may not vary accordingly. For example, at Conne River marine survival actually decreases with increased smolt length or weight, but increases with smolt condition (Fig. 8). When examined among rivers, patterns are inconsistent with some stocks showing little or no apparent link between survival and size (length or condition; Fig. 9, 10) (e.g Highlands River), while other rivers show either increasing (e.g. Campbellton) or decreasing (e.g. Conne River, Northeast Brook, Trepassey) marine survival with increased smolt size

Coupled with the inconsistent associations between smolt run timing and survival, accurate forecasts of subsequent adult salmon returns are difficult, if not pointless, to make. Cramer (2000) states that most recruitment variation in Pacific salmon populations is environmentally driven and that recruitment, and survival of hatchery chinook or coho salmon stocks can vary among years by more than an order of magnitude, both of which are highly influenced by conditions affecting fish while at sea.

CONCLUSIONS

Based on the information and preliminary analyses carried out we conclude that within Newfoundland, survival is highly variable and is generally low. Given the closure of the commercial Atlantic salmon fishery in Newfoundland in 1992, survivals have shown little consistent improvement and, for some stocks (e.g. Conne River, Northeast Brook, Trepassey) are actually lower, on average, since the fishery closed. In most, but not all cases, the 'trend' in survival is downward.

Analyses of smolt biological characteristic information and run timing statistics show no consistent patterns among rivers as these parameters relate to subsequent marine survival. Within individual rivers, higher survival can sometimes be associated with larger smolts, but not in other rivers. Thus, survival appears to be random and not serially correlated among years; often years of moderately high survival have been followed immediately by substantial declines.

We conclude that pre-season forecasts of prefishery abundance of adult Atlantic salmon are difficult to make with any degree of accuracy or consistency. Improvements to this situation will likely not occur given the absence of sound information related to functional relationships of various factors that influence the survival of salmon, particularly those affecting salmon during the ocean phase of their life cycle. We acknowledge, however, that simply looking for correlations, with say, environmental factors will be of limited use. As stated by Walters and Collie (1988), better understanding of how environmental influences can be, or have been confounded by the effects of stock size and fishing are required, and sound, long-term monitoring programs are required to understand thses influences.

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Table 1. Smolt production and marine survival from smolt to adult small salmon, Newfoundland Region. Survival values pertain to the year of adult small salmon return from the previous years smolt class. CV is the coefficient of variation. Data were obtained from O'Connell et al. 2001. All values for 2001 are considered preliminary and were provided by individual researchers.

Year	Campbellton River		Northeast Brook, Trepassey		Rocky River		Conne River		Highlands River		Western Arm Brook	
	Smolts	Survival	Smolts	Survival	Smolts	Survival	Smolts	Survival	Smolts	Survival	Smolts	Survival
1971											5735	
1972											11905	7.1
1973											8484	6.7
1974											11854	6.0
1975											9600	5.4
1976											6232	5.8
1977											9899	6.0
1978											13071	3.2
1979											8349	12.1
1980											15665	5.6
1981											13981	3.1
1982											12477	3.3
1983											10552	9.1
1984											20653	2.2
1985											13417	2.3
1986			1117								17719	3.9
1987			1404	8.1			74585				17029	2.5
1988			1692	6.9			65692	10.2			15321	2.5
1989			1708	3.7			73724	7.6			11407	3.0
1990			1902	4.2	8287		56943	7.3			10563	3.9
1991			1911	5.2	7732	2.5	74645	4.2			13453	2.2
1992			1674	2.6	7813	3.1	68208	3.4			15405	3.6
1993	31577		1849	4.7	5115	3.7	55765	4.0	9986		13435	6.1
1994	41663	9.0	944	5.4	9781	3.1	60762	2.7	10503	1.5	9283	7.1
1995	39715	7.3	792	8.5	7577	3.9	62749	5.8	12160	1.6	15144	8.9
1996	58369	8.1	1749	9.2	14261	4.7	94088	7.2	12383	1.6	14502	8.1
1997	62050	3.4	1829	2.9	16900	3.1	100983	3.4	6776	3.2	23845	3.5
1998	50441	5.3	1727	5.0	12163	2.5	69841	2.9	5922	1.4	17139	7.2
1999	47256	6.1	1419	4.9	8625	2.7	63658	3.4	9634	2.5	13500	6.1
2000	35596	3.8	1740	5.8	7616	3.2	60777	8.1	13120	0.6	12706	11.1
2001	38000	6.0	800	3.2	11000	3.1	74450	2.5	-	0.6	15972	4.4
Average	44963	6.1	1516	5.3	9739	3.2	70458	5.2	10061	1.6	13171	5.4
CV	23.1	32.3	25.8	38.3	34.0	20.2	18.1	47.6	25.9	54.0	29.7	49.0

Table 2. Correlation matrix (Spearman) of smolt production among various Newfoundland rivers. Values in large-bold italicized print are statistically significant.

	Conne	**NE Trepassey**	**Rocky**	**WAB**	**Campbellton**	**Highlands**
Conne	1					
NE Trepassey	0.134	1				
Rocky	***0.627***	-0.027	1			
WAB	***0.600***	-0.200	0.373	1		
Campbellton	***0.929***	0.095	***0.952***	0.667	1	
Highlands	-0.214	-0.190	-0.262	-0.381	-0.286	1

Table 3. Correlation matrix (Spearman) of marine survival of smolt to adult small salmon among various Newfoundland rivers. Values in large-bold italicized print are statistically significant.

	Conne	**NE Trepassey**	**Rocky**	**WAB**	**Campbellton**	**Highlands**
Conne	1					
NE Trepassey	0.426	1				
Rocky	0.546	0.420	1			
WAB	-0.104	0.331	0.547	1		
Campbellton	-0.120	0.548	0.317	0.214	1	
Highlands	0.182	0.012	0.012	-0.374	0.060	1

Table 4. Correlation matrix (Spearman) of median smolt run timing among various Newfoundland rivers. Values in large-bold italicized print are statistically significant.

	Conne	**NE Trepassey**	**Rocky**	**WAB**	**Campbellton**	**Highlands**
Conne	1					
NE Trepassey	***0.594***	1				
Rocky	***0.793***	***0.711***	1			
WAB	***0.738***	0.374	0.577	1		
Campbellton	***0.881***	***0.699***	***0.952***	***0.743***	1	
Highlands	***0.714***	***0.747***	***0.738***	***0.898***	***0.857***	1

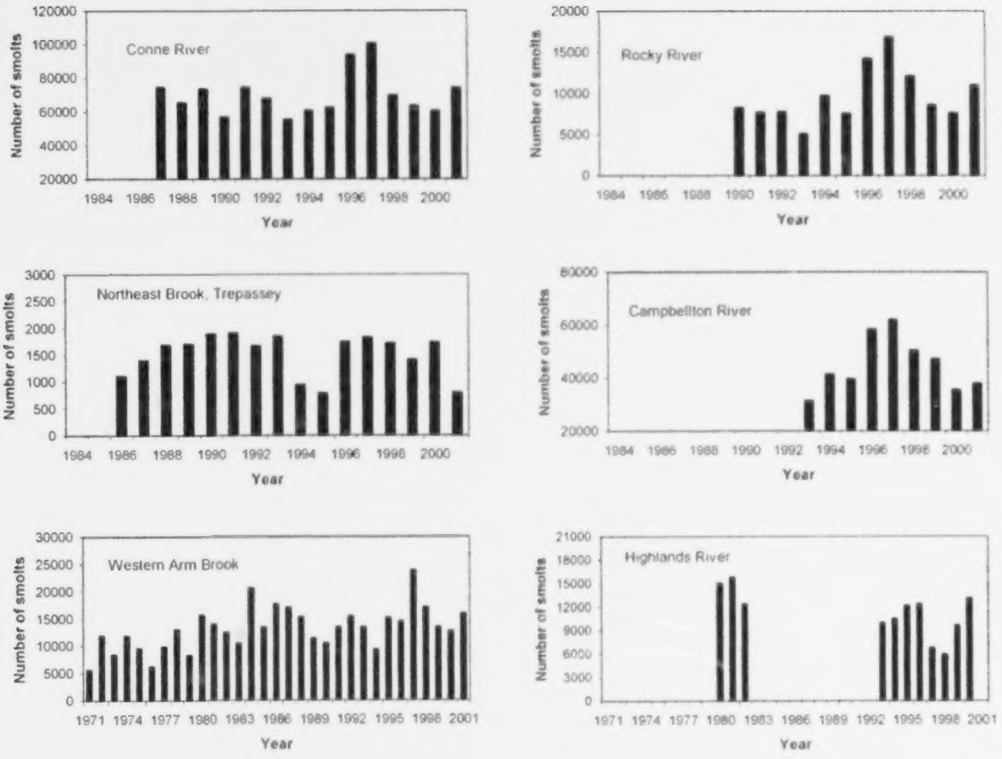

Figure 1. Trends in Atlantic salmon smolt production among various Newfoundland rivers. Data for 2001 are considered preliminary.

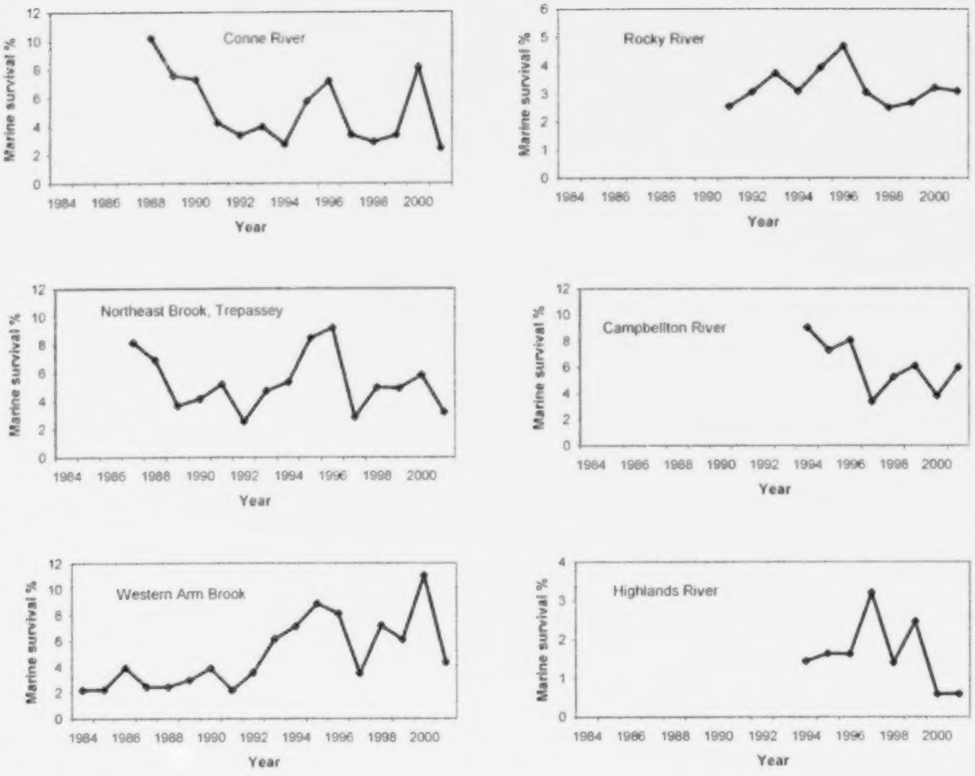

Figure 2. Trends in marine survival, from smolt to adult small salmon returns at various Newfoundland rivers. Corrections have not been made to account for marine exploitation for years proir to 1992. Values for 2001 adult returns are preliminary.

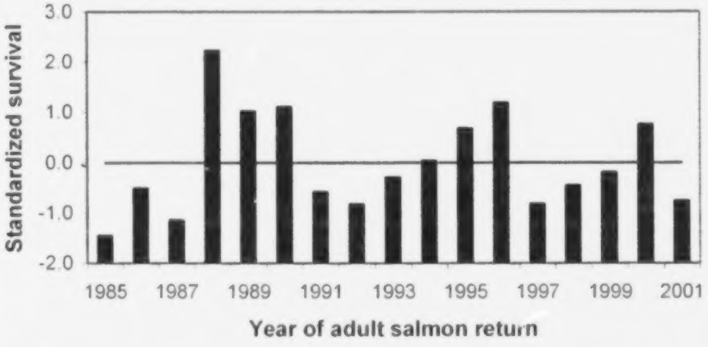

Figure 3. Standardized composite survival of smolt to adult small salmon returns, Newfoundland Region, 1985 to 2001. Data for 2001 are preliminary.

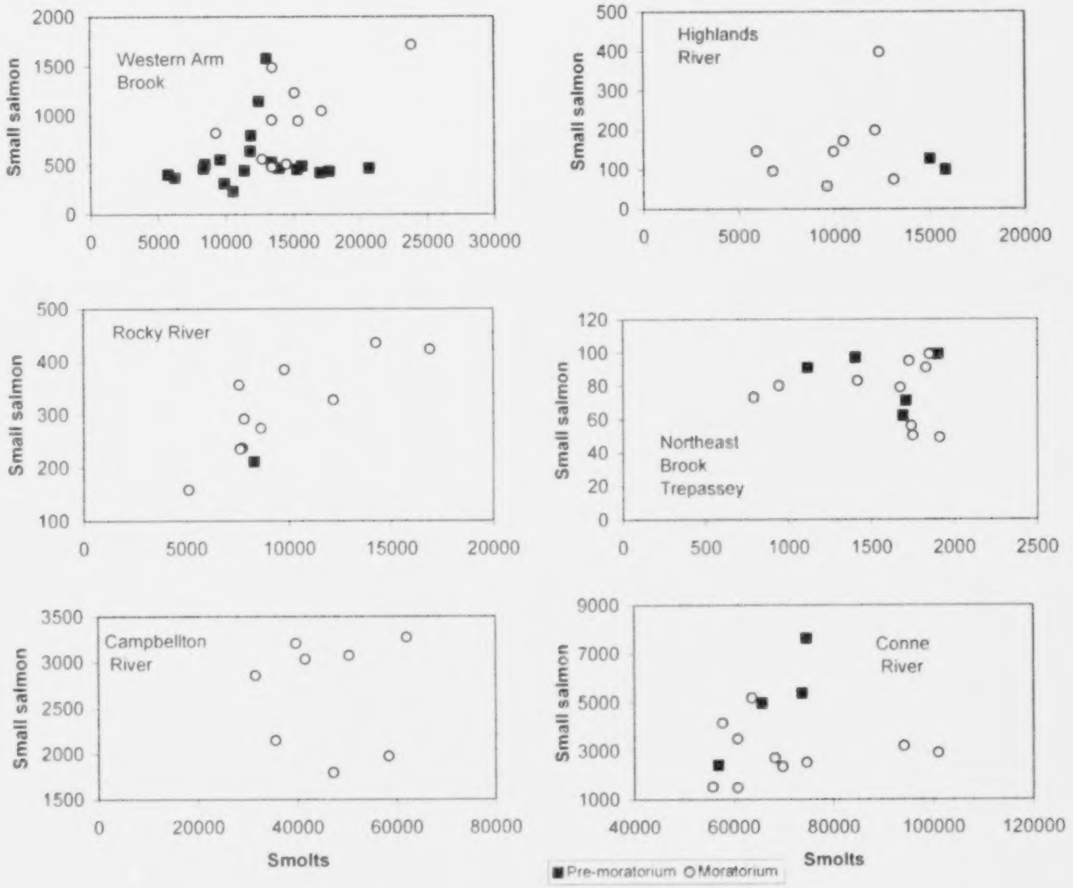

Figure 4. Relationship between smolt production and subsequent return of adult small salmon from various Newfoundland rivers. Moratorium years (1992 to 2001) are shown separately.

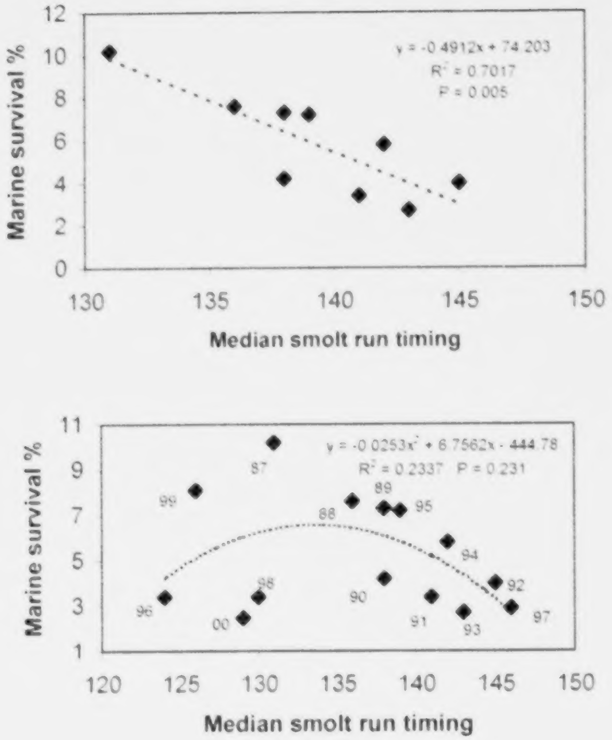

Figure 5. Association between smolt run timing and subsequent survival at Conne River, Newfoundland. Top panel illustrates the period of adult returns from 1987 to 1995. The bottom panel illustrates all years, 1987 to 2001, with the year of the smolt run indicated on the plot.

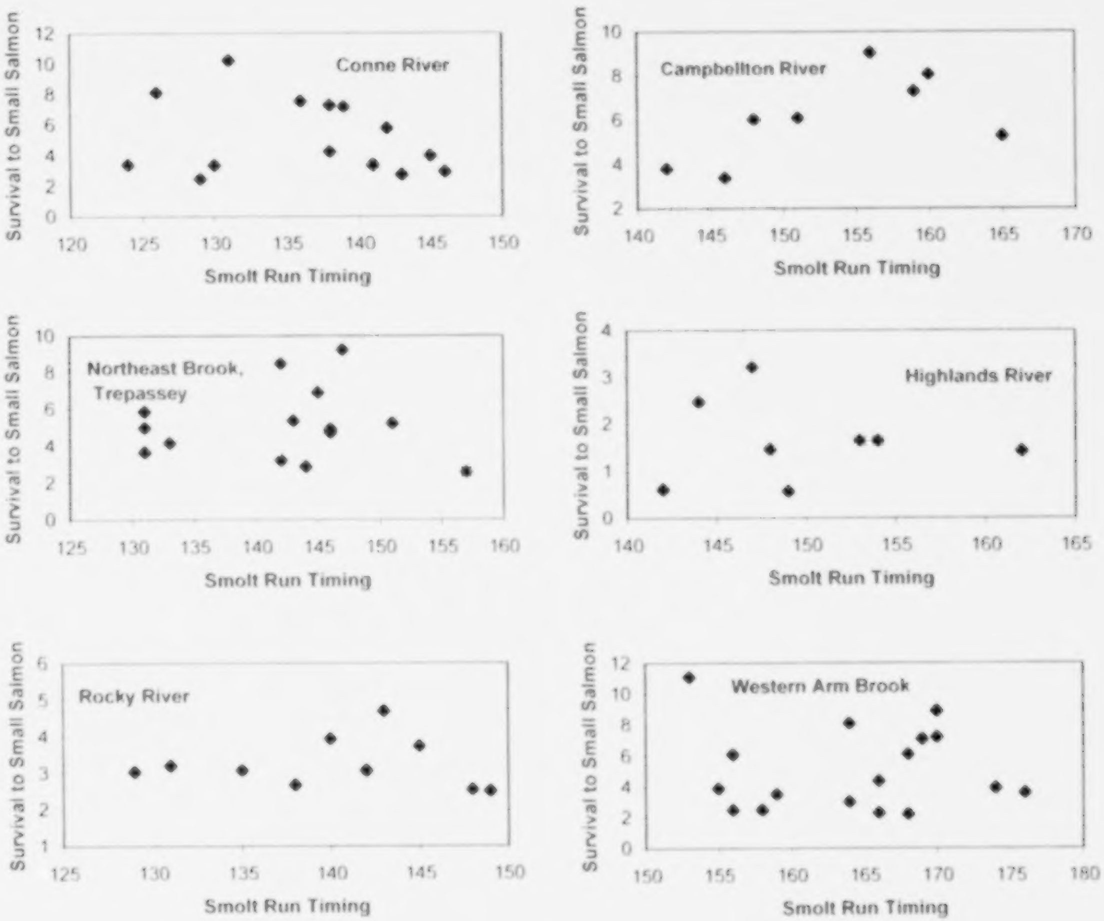

Figure 6. Marine survival versus smolt run timing from various Newfoundland Atlantic salmon rivers. Data, where available, is for the period 1984 to adult returns in 2001. The most recent year (2001) results are considered preliminary.

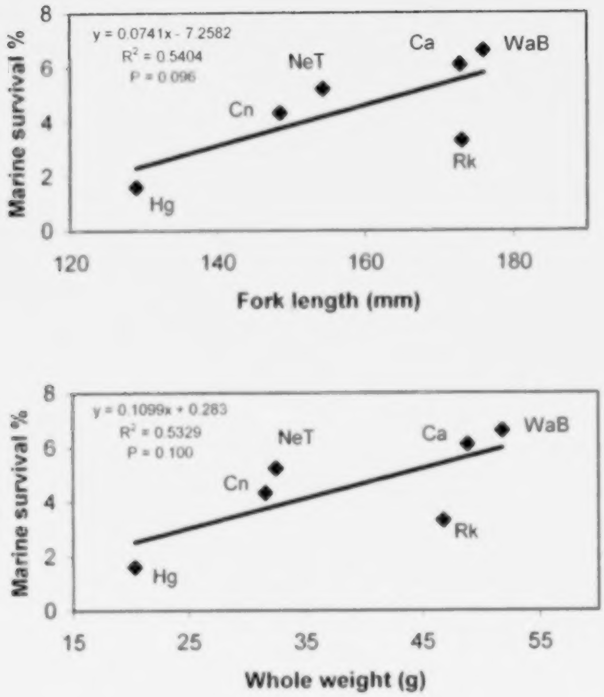

Figure 7. Relationships between marine survival of smolts to adult small salmon versus mean smolt length (top panel) or mean smolt weight (bottom panel). Survivals are for the 1992 - 2001 adult return years only during which time the commercial salmon fishery has been closed. Hg = Highlands River; Cn = Conne River; Net = Northeast Brook, Trepassey, Rk = Rocky River; Ca = Campbellton River, and WaB = Western Arm Brook.

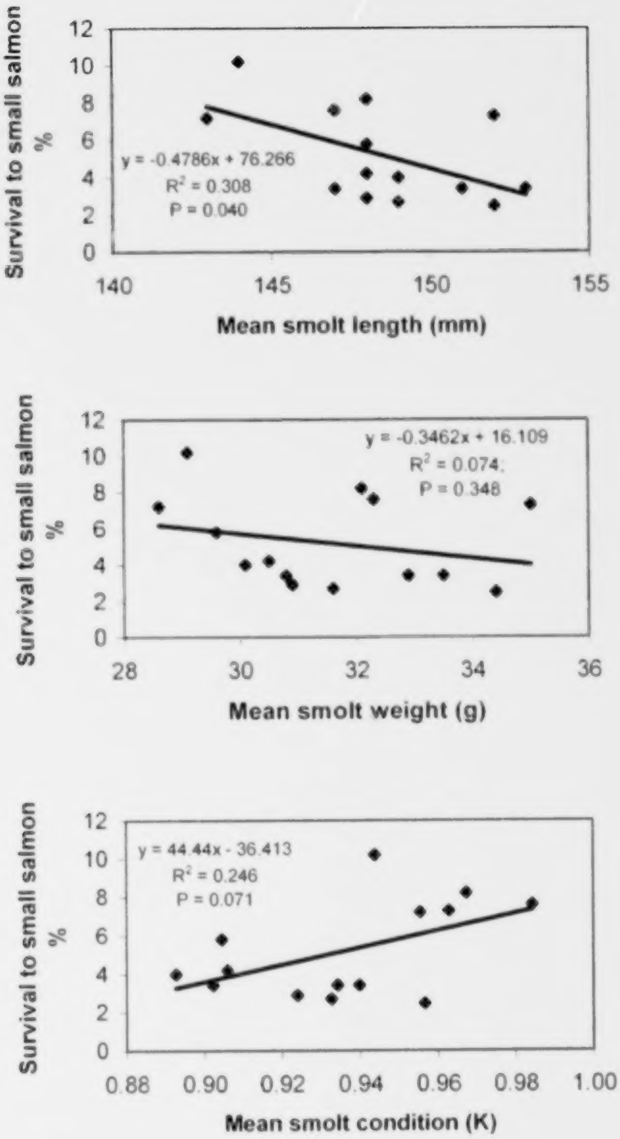

Figure 8. Relationships between smolt length, weight, and condition with marine survival of Conne River Atlantic salmon smolts, for adult salmon returns from 1988 to 2001.

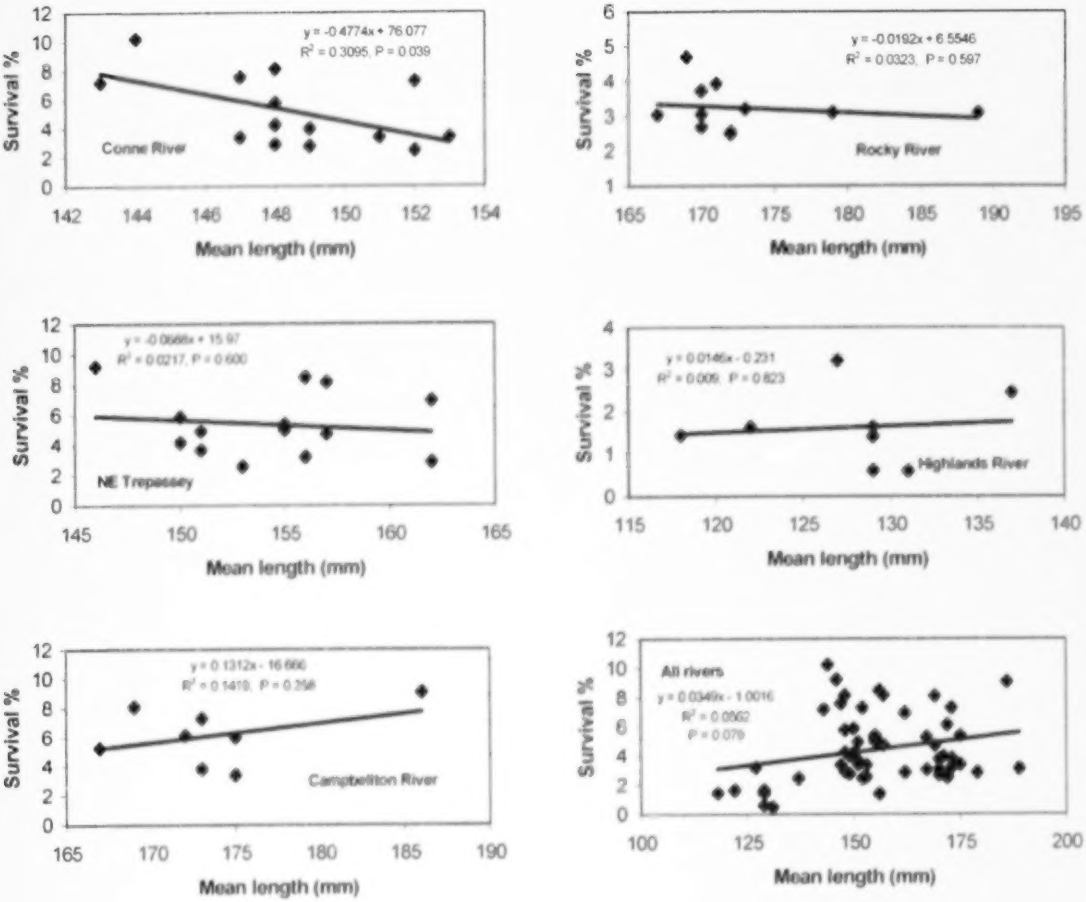

Figure 9. Relationships between marine survival of Atlantic salmon smolts to adult small salmon and mean smolt lengths for various Newfoundland rivers.

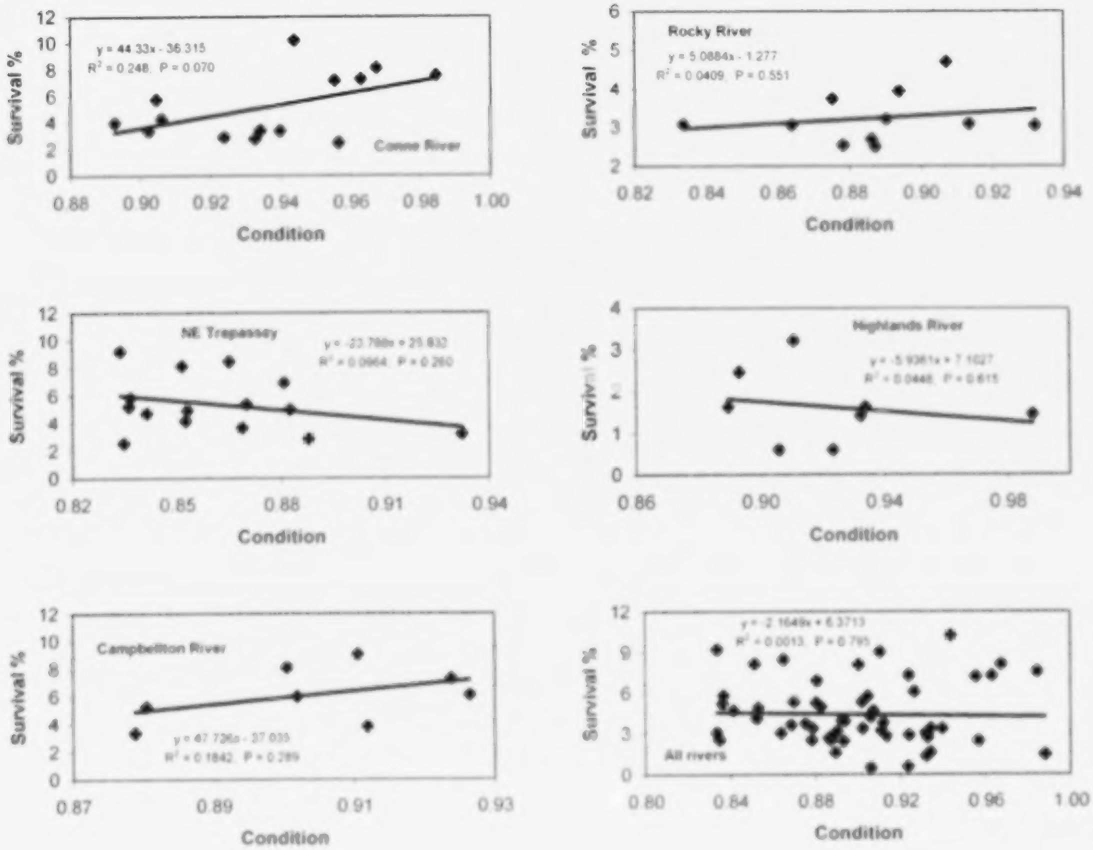

Figure 10. Relationships between marine survival of Atlantic salmon smolts to adult small salmon and mean smolt condition for various Newfoundland rivers.

3

TRENDS IN MARINE SURVIVAL OF HATCHERY-ORIGIN ATLANTIC SALMON (*Salmo salar* L.) TO FOUR MARITIME RIVERS WITH COMPARISONS TO INDICES OF WILD-ORIGIN SMOLT SURVIVAL TO THE LAHAVE RIVER, NOVA SCOTIA, CANADA

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INTRODUCTION

Records of hatchery produced Atlantic salmon (*Salmo salar* L.) juveniles and smolts released to rivers of the Maritime Provinces have been kept since the beginnings of hatchery operations in Canada. Returning salmon from stocking programs were, however, only periodically counted and assessed. Since the establishment of salmon development and enhancement programs in the early 1970s consistent records of returns of marked hatchery-grown fish have been kept for at least four monitoring facilities on the Atlantic coast of the Maritime Provinces. Consistent records were possible because counting facilities were established in fish passage devices installed at impassable barriers to upstream fish migration. The record of returns of salmon combined with knowledge and sampling of downstream migration and fisheries have provided records of trends in the marine survival of hatchery smolts stocked at or above these facilities.

Interpretation of trends in hatchery reared smolt-to-adult return rates has been confounded by change in marine fisheries for salmon, e.g. the Salmon Management Plan of 1984 and 1985, as well as by changes in by-catch regulations for salmon in marine fisheries gear directed to capture other species. Also, changes in rearing practices for hatchery-grown smolts e.g. from two-year to one-year old smolts in the early 1980s, have further complicated the interpretation of trends in return rates. Nonetheless, hatchery smolt return rates have been estimated annually and used in analysis of trends in marine survival of salmon to these facilities (e.g. DFO 1999).

The purpose of this document is to review trends in hatchery smolt survivals in four rivers of Atlantic Canada where hatchery-grown Atlantic salmon smolts have been released and returns monitored annually since 1972 by (Harvie and Amiro 1996: Amiro et al. 1998). Correlation among trends in survival of hatchery smolts to four counting facilities will be examined. Correlation in survival with an index of marine salmon habitat will also be reviewed. On the LaHave River trends in hatchery-smolt to river-return will be compared with trends in wild smolt to wild adult river-returns. The relationship between return rate of wild smolts and average smolt length as well as population size and smolt size will be examined. The questions addressed in this analysis are: 1) Is there a trend among survival indices within these time series? 2) Is marine survival of wild and hatchery salmon correlated in the LaHave River time series?

METHODS

In this analysis annual marine survivals of hatchery origin smolts, stocked in their river of origin, were derived from annual stocking records and annual counts of salmon ascending fishways. These data are available from the records of the Diadromous Fish Division of the Department of Fisheries and Oceans. Marine survivals of hatchery smolts were available for four facilities (Fig. 1). The facilities were: Morgans Falls on the LaHave River (1974 – 2000); the Barrier Dam below Ruth Falls on the East River Sheet Harbour (1975 – 2000); Liscomb Falls of the Liscomb River (1978 – 1998); and Mactaquac Dam on the Saint John River (1974 – 2000).

Hatchery smolt release information at or above these facilities provided information to estimate annual return rates of hatchery salmon after one winter at sea (1SW) and two (2SW) or more (MSW) winters at sea (Table 1) (Marshall et al. 2000; Amiro et al. 2000; DFO 2001). Removals below the fishway were accounted for in estimating annual return rates to the Saint John River only.

Downstream migrating wild and hatchery salmon smolts have been counted at a hydroelectric facility opposite to the Morgans Falls fishway since 1996. Migrating smolts are deflected to an assessment area from the turbine intake by surface to bottom louver deflectors. Estimates of annual wild smolt migrations above Morgans Falls on the LaHave River were derived by mark and recapture methods using counts of wild and marked hatchery smolts made at the downstream assessment facility. Fork length and scale samples were collected on every twentieth wild smolt. Differentially marked hatchery smolts were released 2.0 km above the counting facility on three to four occasions throughout each smolt migration season. The remainder of the adipose clipped hatchery smolts was released in the tributaries above the fishway prior to 1998 and into the fishway since 1998. Because the mean estimated downstream mortality of smolts at that facility in 1997 was 2.6% (Amiro and Jansen 2000) no adjustment for downstream mortality attributed to the power facility was made to the data used to estimate survival rates in this analysis.

In addition to count information, scales were collected at the Morgans Falls Fishway. Scales provided age interpretations for individual fish. Ages of fish and total counts enabled the construction of a cohort-based (returns aggregated by egg deposition year) stock and recruitment table. Stock was based on total number of spawning fish in year-i and recruits were the numbers of first spawning wild salmon, year i+3 to i+5, that resulted from an egg deposition year, i.e. cohorts. The modal age of wild smolts above Morgans Falls is two years.

Annual indices of the February marine habitat area for salmon (ICES 2001) were used as a marine environment indicator. This index is a summation of the area of 2^0 arc squares of the North Atlantic where temperatures were between 0 and 14^0 C weighted by a thermal habitat preference probability distribution derived from research drift-netting for salmon at sea (Reddin and Friedland 1993).

Habitat and survival variables were standardized to their respective means for plotting purposes. Variables were not log transformed to stablise residuals as done by Harvie and Amiro (1996) and therefore no fitted coefficients or error estimates are reported for these analyses.

Trends in survival were evaluated by cumulative sum differences (Woodward and Goldsmith 1964) and by correlation, regression and analysis of covariation using SYSTAT V8.0

RESULTS

Patterns of annual survivals of hatchery smolt to 1SW and 2SW adult returns to LaHave River, East River Sheet Harbour, Liscomb and MSW hatchery returns to Saint John River at Mactaquac (Table 1) were somewhat dissimilar prior to 1987. Only the LaHave and Liscomb River return rates were significantly correlated for 1SW (p=0.004) and 2SW (p=0.038) fish for the entire time series.

Collectively since 1974 (by ANCOVA), there was a significant ($p<0.001$) negative trend in 1SW survivals among rivers. Since the 1987 smolt year the rates have been lower at all facilities (Fig. 2). However, only the Saint John River and Liscomb River had significant ($p<0.005$) negative trends in hatchery smolt survival to 1SW. Since 1987, there was a significant ($p=0.003$) common trend for 1SW fish and there were no significant ($p<0.091$) differences among rivers.

Collectively since 1974, survival of hatchery smolt to 2SW or MSW return was also significant ($p<0.001$) among rivers but some trends were significantly ($p<0.001$) different. Since the 1987 smolt year the rates have been lower at all facilities (Fig. 3). Since 1987, there was a significant ($p=0.009$) common trend for 2SW or MSW fish and there were no significant differences among rivers.

Similarities in trends were visually identifiable from plots of the cumulative sum of differences from their respective means by river and sea-age class (Fig. 4 and 5). By this statistic, trends in annual hatchery return rate by river tracked similarly among three rivers. However, striking dissimilarities were observed for both 1SW and MSW salmon in the Saint John River.

The Salmon Habitat Index (SHI) tracked the decline in survival of hatchery smolts early in the data series but smolt survivals did not increase with increasing SHI since 1997. Only the Saint John River 1SW ($p=0.011$) and 2SW ($p=0.003$) hatchery smolt survivals were correlated with the February SHI in the first winter at sea. SHI was not a significant variable in the multiple-correlation analysis.

Estimates of wild smolt migrations were derived from mark and recapture information at Morgans Falls, LaHave River. The numbers of marked smolts released were approximately 4,000 annually and the numbers of smolts examined at the facility ranged from 10,000 to 25,000 annually. These data resulted in precise smolt estimates (Fig. 6). Return rate to 1SW for wild smolts ranged from 1.4% to 4.8%. Relative to hatchery smolts, wild smolts were 4.8 to 6.7 times more likely to return during the 1996 to 2000 period. Based on only five data pairs the relationship between hatchery and wild return rates to 1SW was significant ($R^2=0.85$, $p=0.025$) (Fig. 7). Annual mean smolt length was not correlated with the numbers of smolts produced (Fig. 8). Return rate of wild smolts to 1SW salmon was not correlated with the annual mean smolt length (Fig. 9). Egg to smolt survival above Morgans Falls varied between 0.8% to 1.4% (Fig. 10).

The decline in wild salmon survival, as indicated by the regression of LnR/S on Year, to the LaHave River above Morgans Falls was significant ($p<0.0001$). The natural logarithm of total (1SW, 2SW and 3SW) survival of hatchery salmon to Morgans Falls was used for comparison to the Ln(R/S). The decline in natural logarithm of survival of hatchery smolts stocked above Morgans Falls was significant ($p=0.022$). There was also a significant ($p=0.024$) decline in Ln(Survival) of hatchery smolt released in and returned to the Liscomb River since 1970 (Fig. 11).

There was no significant ($p=0.129$) trend in the return rate of hatchery smolts after 1SW to Morgans Falls on the LaHave River, 1974 to 1999. It is not possible to show a significant ($p=0.997$) long term effect of the Management Plan of 1985 on hatchery smolt to 1SW return to Morgans Falls. The mean percent survival for the Pre-Plan was 1.59% (Std. Error=0.35) and the Post-Plan mean survival was 1.59% (Std. Error=0.28). There was no significant ($p=0.503$) trend in the return rate of hatchery smolts in the Pre-Management Plan period, however, the trend was significant ($p=0.007$) and negative in the Post-plan period (Fig. 12).

The recruitment rate of wild salmon on the LaHave River above Morgans Falls was significantly ($p=0.0004$) different between the Pre- and Post-Management Plan periods. The mean Ln(R/S) was 0.30 (Std Error 0.11) during the Pre-period and –0.27 (Std. Error 0.09) during the Post-period. The rate of decline (trend slope) was significantly ($p=0.010$) different between the Plan periods (Fig. 12). Negative trends were significant for wild fish in the Pre- ($p=0.005$) and Post- ($p=0.020$) Management Plan periods. The rate of decline in the Ln(R/S) was less in the Post-Management Plan period.

DISCUSSION

Analysis of trends in survival of hatchery stocked smolts in the four rivers indicated considerable agreement among rivers. Survival rates have been consistently below mean values since 1987 for the LaHave, East and Liscomb rivers and since 1981 for the Saint John River.

A reason for the difference in the Saint John River profile may be the different marine migration (Ritter 1989) and/or in the full accounting of removals below the fishway in the Saint John River data series relative to other data sets. Returns to Morgans Falls fishway were used in this analysis because a similar accounting for wild salmon has not been made and therefore the data are more comparable between hatchery and wild returns to the LaHave River above Morgans Falls.

The SHI has declined since the peak noted in 1982 with two episodes of increases, 1985 to 1989 and 1997 to 1999. In contrast to the results reported by Harvie and Amiro (1996) only the Saint John River hatchery smolt return rates remained significantly correlated with the SHI. Although Harvie and Amiro (1996) may have used different months of the SHI they also showed that SHI monthly values were highly correlated. No attempt to maximise R^2 was attempted in this analysis.

The data and analysis indicated that wild recruitment rate prior to the Management Plan of 1985 had been declining and continued to decline after 1985, albeit at a lower rate. After the 1985 Management Plan the wild smolt return rate continued to decline, variation in the hatchery smolt return diminished and a declining trend began for hatchery-origin smolts. The 1985-year was chosen *apriori* as the break point for this analysis only because of the potential effects of the Management Plan instituted in 1984, and strengthened in 1985 with the complete closure of local commercial salmon fisheries. No statistical breakpoint could readily be determined from the data.

Hatchery smolt-to-first-return survival rates have been used to test variables affecting survival among rivers (Harvie and Amiro 1996). Other than for fish returning after one winter-at-sea to the LaHave River no significant ($p<0.05$) effects were found for the Canadian Salmon Management Plan introduced in 1984 and effectively closing the local fisheries in 1985. The Salmon Management Plan and the North Atlantic Salmon Conservation Organization (NASCO) agreements concerning the distant fisheries of Greenland and Canada initiated at about this time, were intended to reduce high seas interception of salmon. These fisheries were thought to be contributing to the decline in return of Atlantic salmon to rivers of North America and Europe. In North America these plans were designed to substantially reduce or eliminate exploitation in all fisheries for two-sea-winter (2SW) salmon and to concentrate fisheries exploitation on one-sea-winter salmon in rivers where returns were expected to be greater than spawning requirements. The Harvie and Amiro (1996) analysis indicated differing results among hatchery-supplemented rivers and ages of salmon. However, the analysis also indicated a general decline in marine survival. This general decline continued after an initial increase in survival that followed implementation of the Plan. Also, marine survival was marginally more associated with indices of marine salmon habitat than a simple negative temporal trend.

Declining trends in hatchery returns have been coincident with declines in wild salmon counts in some locations of the Maritimes Atlantic coast (Amiro et al. 1998). Declines in wild smolt survival to rivers in Newfoundland were noted prior to the Newfoundland Atlantic salmon commercial fishing moratorium initiated in 1992 after which survival rates increased (Dempson et al. 1998). Survival rates of wild smolts returning to Newfoundland rivers have been unstable but generally lower since 1997 (Dempson et al. 2001). Similar declines were noted in survivals of wild salmon to rivers in Quebec, e.g. Bec-Scie and de la Trinité (Tremblay et al. 2001). These data and analyses together with published assessment information suggest the decline in marine survival is widespread, especially for 2SW and older salmon and since 1987, is lower and spatially variable for 1SW fish.

The use of hatchery smolt survival as an indicator of wild smolt survival has often been questioned because of the possible biases introduced by broodstock selection, juvenile rearing and release. The ages of LaHave River broodstock and smolt have varied over time and could have affected the proportions of 1SW and 2SW in the hatchery component. Also, prior to 1980 some two-year-old smolts were included in annual releases. However, during those years, on average, four times the number of one-year-old smolts was stocked for every two-year old smolt in the LaHave River. After 1979 only one-year-old smolts were stocked. Prior to 1997 the selection of broodstock was sometimes biased to salmon of older ages. As a result, in comparison to wild returns, hatchery returns were sometimes biased to older age salmon in the counts at Morgans Falls, LaHave River. However, substantial numbers of younger aged fish were also selected for broodstock and were spawned with older salmon and provided a consistent recruitment of 1SW hatchery salmon. The results of this analysis suggest that these factors collectively may have added error to the relationship and did result in a bias between wild and hatchery smolt performance in favor of wild smolts. However, changes in the slopes of hatchery survival since 1985 suggest that hatchery smolts performed better relative to wild smolts, both in offset and variance in return rate, prior to 1985.

While the time series of hatchery smolts did have inconsistencies these results suggest that those random events during the marine phase and not pre-condition of smolts in freshwater substantially influenced the return rates of wild and hatchery smolts simultaneously. At Morgans Falls, LaHave River, wild smolt return was offset from hatchery smolt return by a factor of 6.9 for the 1996 to 2000 time period but the direction and severity of the decline in return rate was the same as for wild smolts. This analysis suggested that the survival of hatchery smolts in the marine environment, although offset to a considerable amount from wild smolt returns, was a reliable index of the relative performance of wild smolts. These results suggested those longer-term indices of wild and hatchery smolt survival can be useful for interpreting trends in wild smolt survival.

Acknowledgements

Many people contributed to the process of collecting, collating, and organizing the data necessary to perform these analyses. Personnel of the Diadromous Fish Division, especially Debbie Stewart, provided annual tallies of the distributions of hatchery products. Eric Jefferson and David Longard collected and processed the wild and hatchery smolt data. The assistance of the Morgan Falls Power Company for access to their facility and assistance with processing fish at their facility was greatly appreciated. The assistance of the LaHave River Salmon Association in operating both the downstream and upstream facilities at Morgan Falls contributed to the data necessary to perform these analyses. Dr. Larry Marshall provided data from the Saint John River as well as valuable discussion and review of the analysis. Ms. Carolyn Harvie provided suggestions that clarified the statistical analysis.

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Table 1. Numbers of recruits per spawned fish (R/S, aligned to the age-two smolt year) above Morgans Falls, LaHave River. Annual percent survival (aligned by year of smolt migration) after one and two winters at sea for hatchery smolts stocked at and returning to the LaHave River at Morgans Falls; to East River Sheet Harbour (ERSH) at Ruth Falls; to the Liscomb River; and for age-one, -two and older Atlantic salmon to the Saint John River (SJR) above Mactaquac Dam, 1974 to 1999. The salmon habitat index (SHI) for February in the North Atlantic Ocean is also shown.

Smolt	LaHave	(%) Survival to return after first sea-winter				(%) Survival to return after two+ sea-winters				SHI
Year	Ln(R/S)	LaHave	ER SH	Liscomb	SJR	LaHave	ER SH	Liscomb	SJR	February
1974	1.136	0.90			1.89	0.14			0.68	1862
1975	1.024	3.37	0.32		2.80	0.24			0.84	1827
1976	0.356	1.85	0.60		2.35	0.37	0.03		0.85	1676
1977	-0.081	0.84	0.25		1.04	0.15	0.02		0.41	1915
1978	0.279	1.42	0.23	1.23	1.95	0.70	0.01	0.14	1.53	1951
1979	0.437	1.48	0.39	2.09	4.42	0.81	0.02	0.10	1.12	2058
1980	0.147	1.90	0.64	1.07	2.42	0.18	0.01	0.18	0.76	1823
1981	-0.077	1.98	0.64	2.14	1.61	0.17	0.02	0.16	0.58	1912
1982	-0.140	0.93	0.15	1.42	0.91	1.23	0.00	0.10	0.56	1703
1983	-0.023	1.27	0.74	0.61	0.98	0.31	0.10	0.08	0.55	1416
1984	-0.263	1.37	0.67	0.39	0.92	0.71	0.04	0.22	0.35	1257
1985	-0.013	4.19	0.09	2.91	0.87	1.74	0.01	0.18	0.45	1410
1986	0.259	2.40	0.10	3.08	1.17	0.21	0.09	0.23	0.35	1688
1987	-0.026	3.92	2.47	1.58	0.67	0.99	0.03	0.23	0.33	1627
1988	0.071	1.62	0.46	0.63	0.76	0.31	0.04	0.05	0.17	1698
1989	-0.084	1.93	0.60	1.75	0.40	0.22	0.06	0.08	0.17	1642
1990	-0.567	0.42	0.16	0.84	0.65	0.17	0.01	0.05	0.26	1503
1991	-0.336	3.60	0.07	0.53	0.69	0.46	0.01	0.05	0.12	1357
1992	-0.583	0.83	0.15	0.44	0.41	0.23	0.05	0.03	0.21	1381
1993	-0.561	0.56	0.21	0.59	0.39	0.21	0.00	0.03	0.21	1252
1994	-0.125	1.05	0.32	0.38	0.66	0.22	0.01	0.02	0.27	1329
1995	-0.623	1.38	0.36	0.64	1.14	0.20	0.02	0.03	0.19	1311
1996	-0.528	0.31	0.37	0.17	0.56	0.14	0.06	0.00	0.08	1470
1997	-0.188	0.87	0.07	0.14	0.75	0.17	0.00	0.00	0.20	1594
1998	-0.411	0.31	0.03	0.03	0.56	0.11	0.01		0.06	1849
1999		0.72	0.05		0.46	0.27	0.01			1741
2000										1634
2001										1685

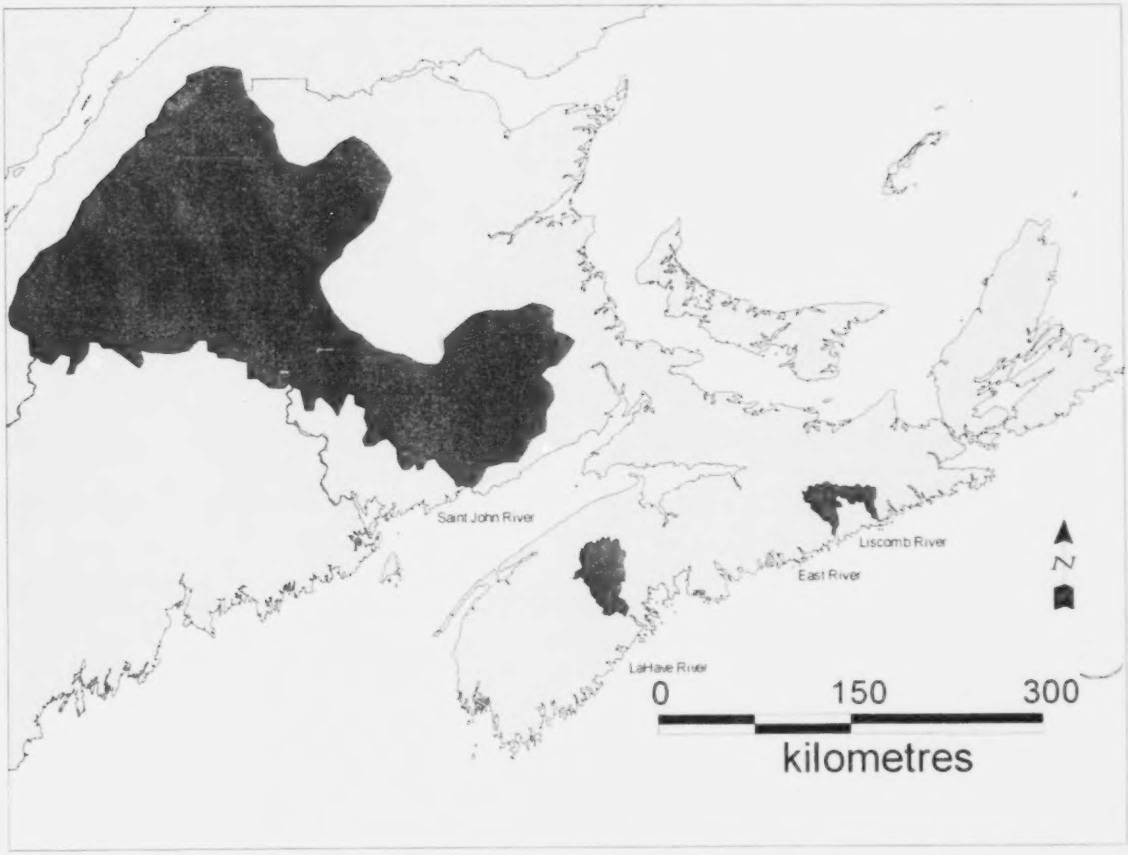
Saint John River
Liscomb River
East River
LaHave River
N
0
150
300
kilometres

Figure 1. Locations of four rivers where annual counts of salmon were conducted, 1974 to 2000.

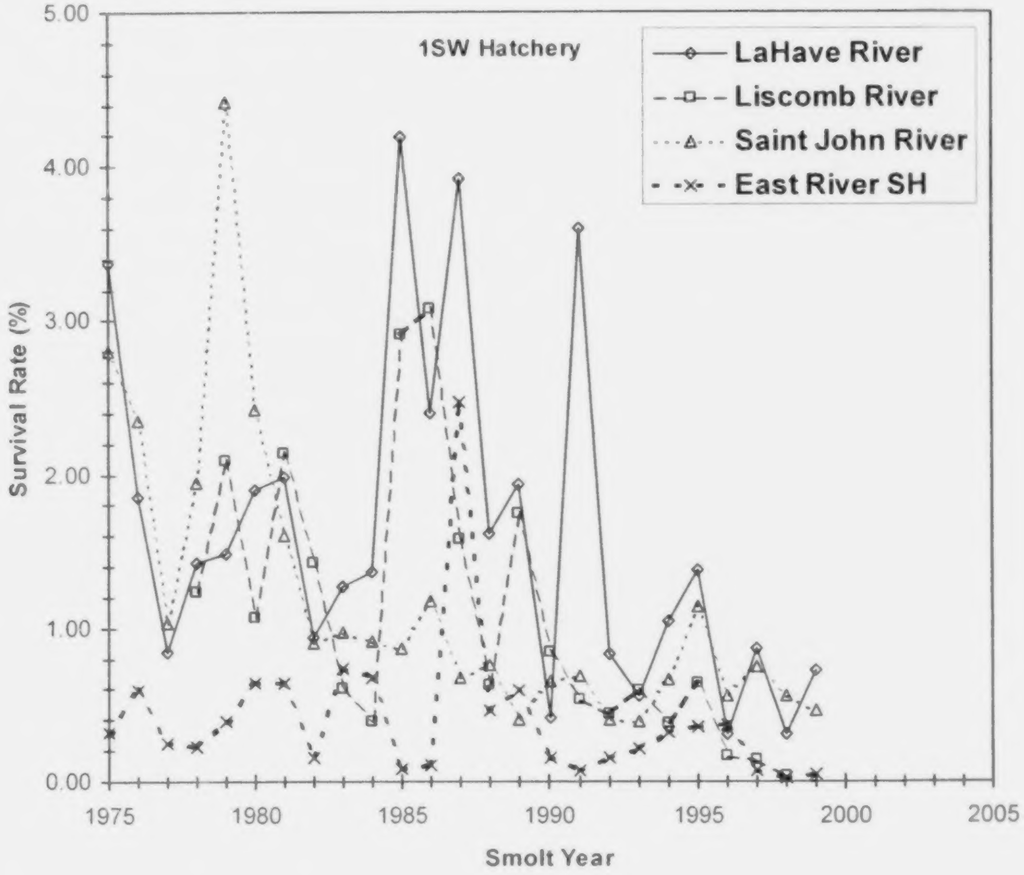

Figure 2. Atlantic salmon hatchery smolt-to-return (%) after one winter at sea for LaHave River, Liscomb River, Saint John River, and East River Sheet Harbour, 1975 to 1999.

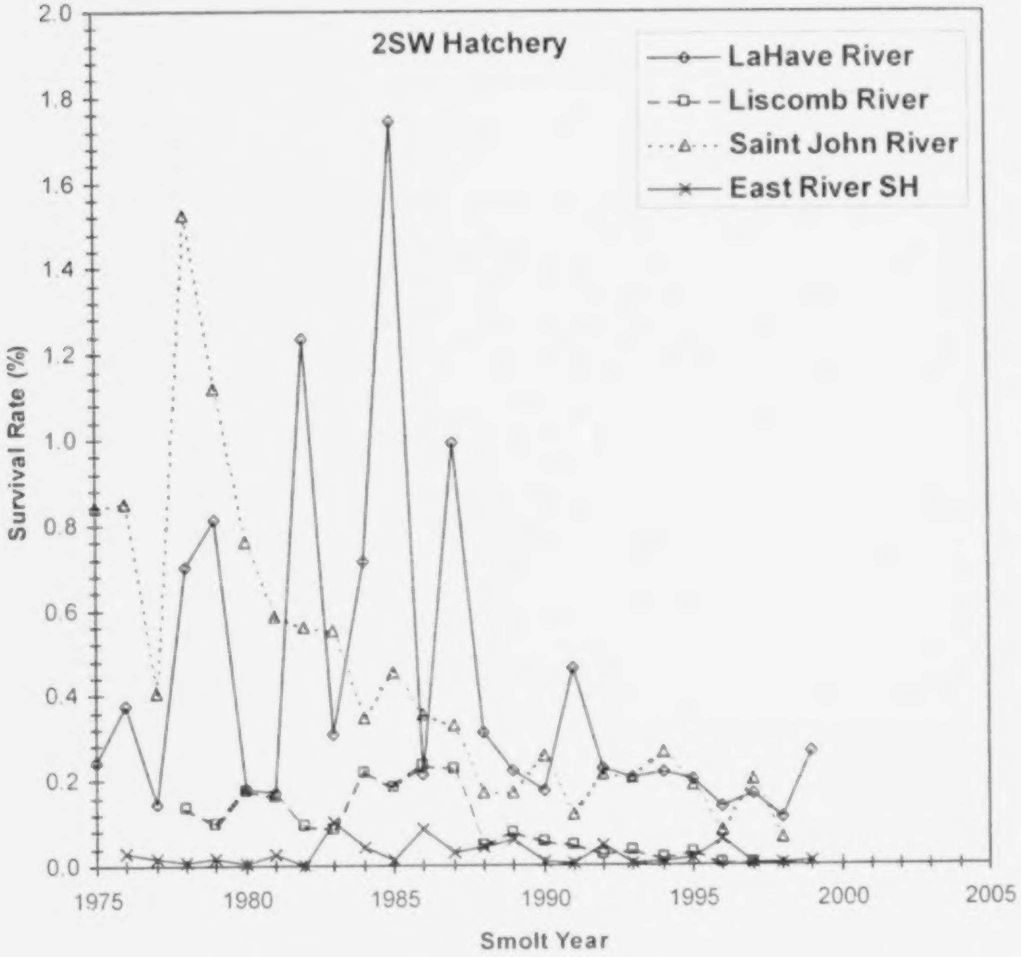

Figure 3. Atlantic salmon hatchery smolt-to-return (%) after two winters at sea for LaHave River, Liscomb River, East River Sheet Harbour, and after more than one winter for the Saint John River, 1975 to 1999.

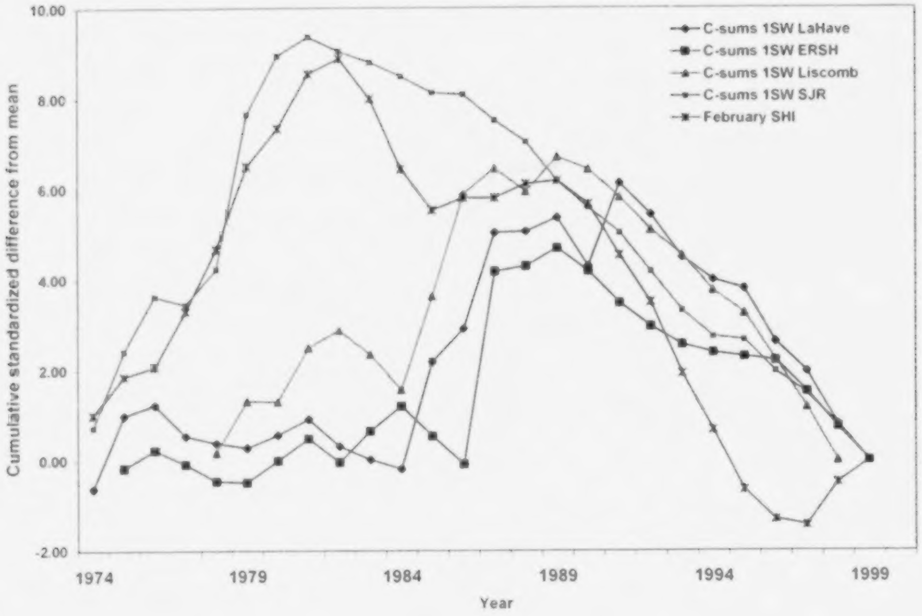

Figure 4. Plot of the cumulative standardized difference from mean return rates of one-sea-winter Atlantic salmon of hatchery origin to four rivers, LaHave River at Morgans Falls, East River Sheet Harbour, Liscomb River and Saint John River at Mactaquac Dam, smolt years 1974 to 1999.

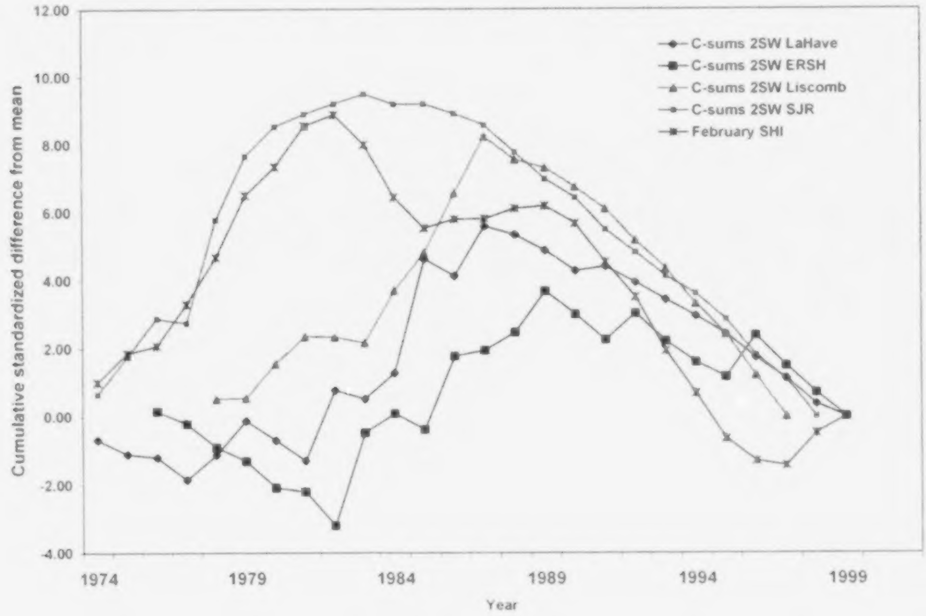

Figure 5. Plot of the cumulative standardized difference from mean return rates of two-sea-winter Atlantic salmon of hatchery origin to four rivers, LaHave River at Morgans Falls, East River Sheet Harbour, Liscomb River and Saint John River at Mactaquac Dam, smolt years 1974 to 1999.

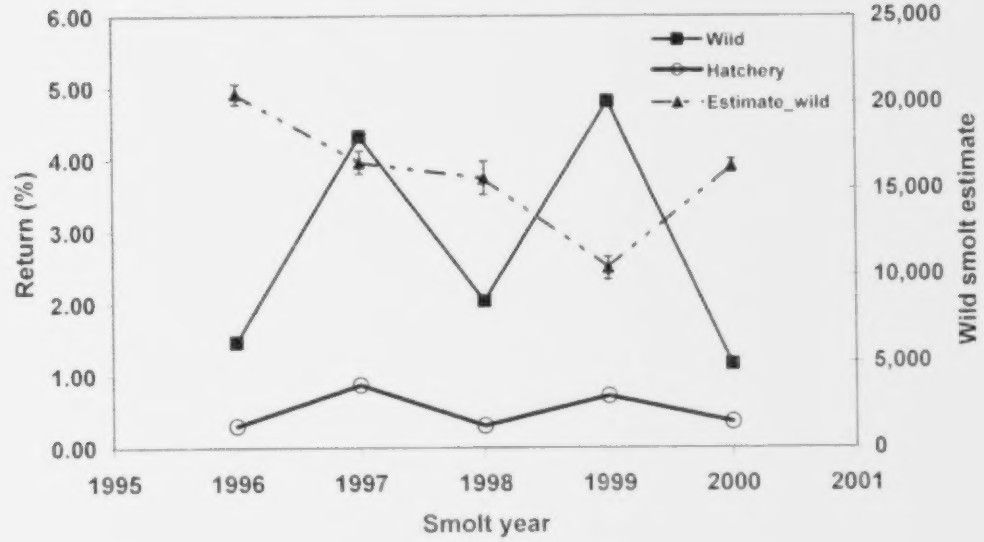

Figure 6. Number and return rate (%) after one winter at sea of wild Atlantic salmon smolts and hatchery smolts counted or stocked above Morgans Falls, LaHave River by smolt year 1996 to 2000. Median (▲) and 90% confidence ranges of the wild smolt population estimates are shown.

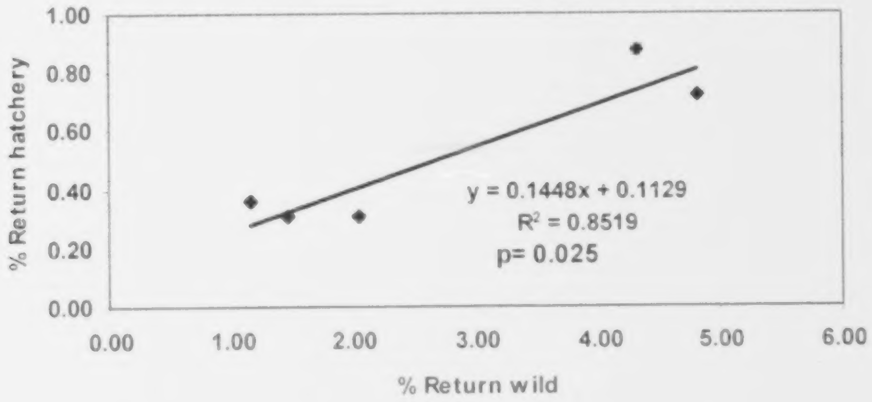

Figure 7. Relationship between return rate of hatchery and wild Atlantic salmon after one sea winter which were counted or released as smolts at or above Morgans Falls, LaHave River, 1996 to 2000.

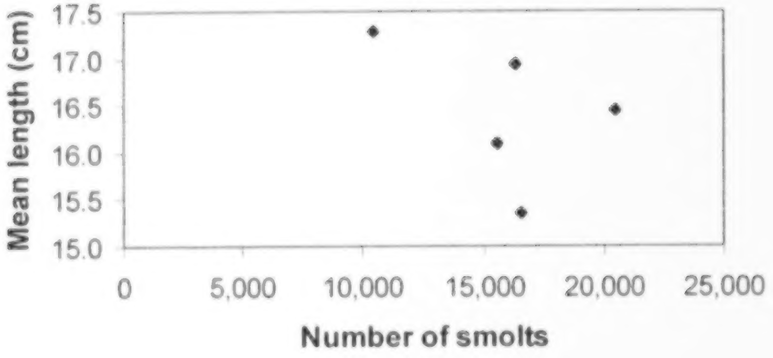

Figure 8. Plot of the mean smolt length (cm) and the numbers of wild Atlantic salmon smolts estimated migrating from above Morgans Falls, LaHave River, 1996 to 2001 (1997 length value is unavailable).

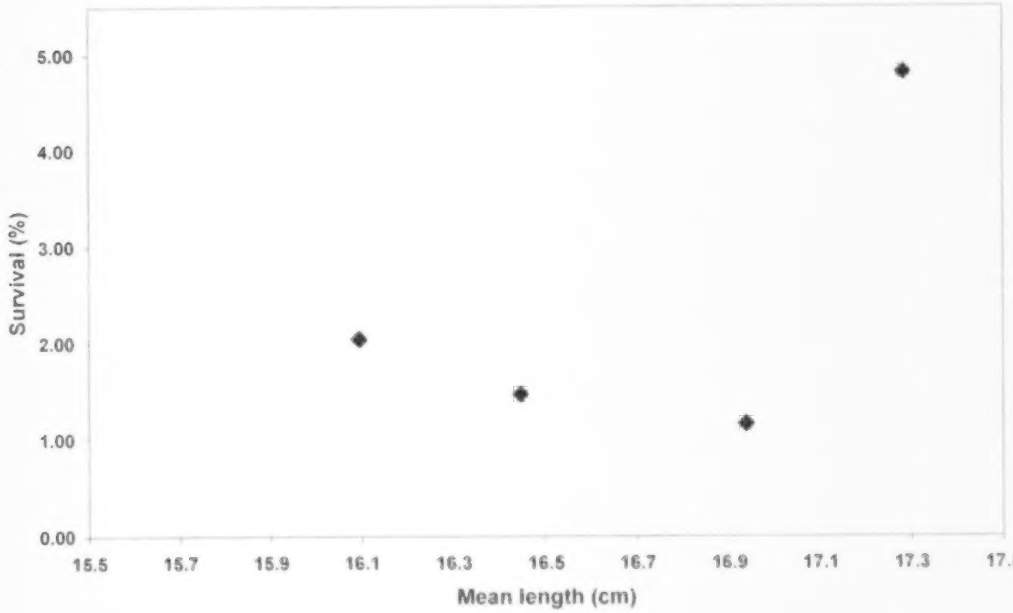

Figure 9. Plot of the percent survival after one sea winter and geometric mean length of wild Atlantic salmon smolts migrating from above Morgans Falls on the LaHave River 1996 to 2000, (1997 length value is unavailable).

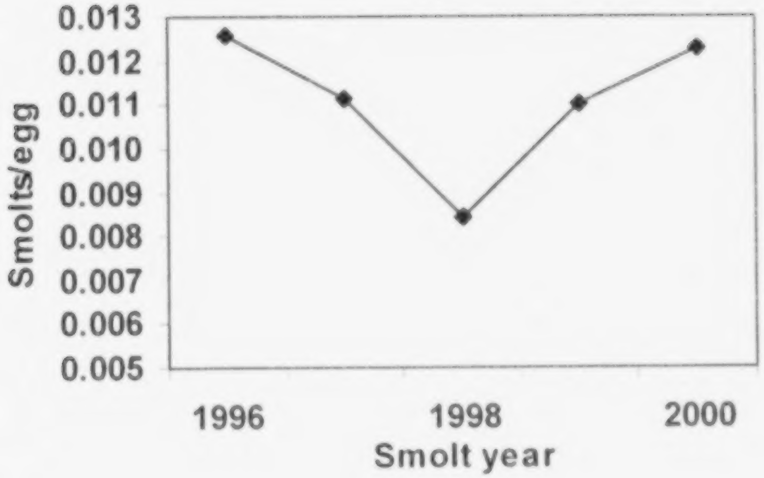

Figure 10. Plot of the number of Atlantic salmon smolts produced in year i+3 of the egg deposition year per egg deposited above Morgans Falls on the LaHave River for smolt migration years 1996 to 2000.

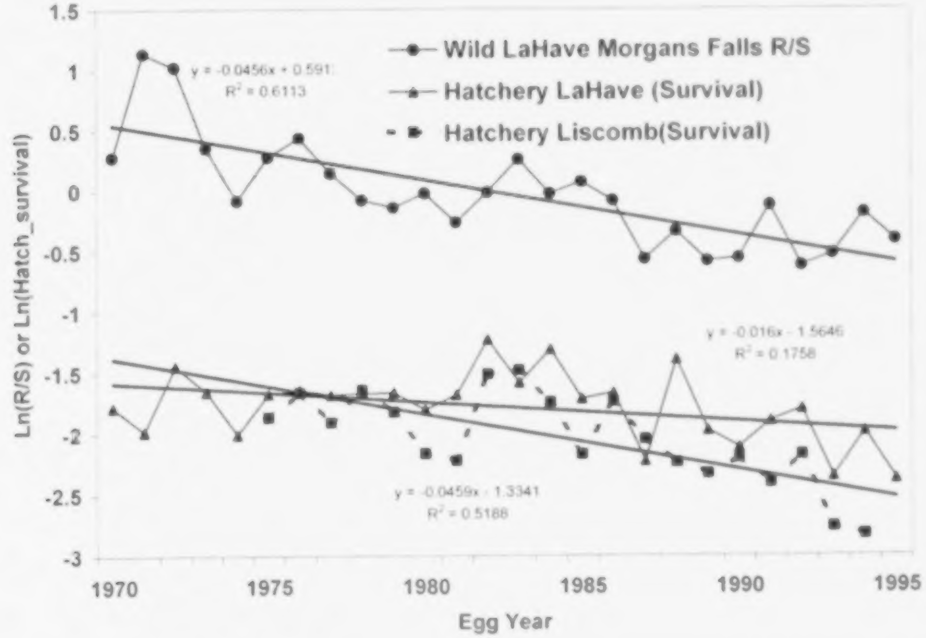

Figure 11. Trends in the natural logarithm (Ln) of recruits per spawned (R/S) Atlantic salmon and return rate of hatchery raised salmon smolts (Hatch_survival) after one- and two-winters at sea for the area above Morgans Falls on the LaHave River and for hatchery smolts stocked in Liscomb River, 1970 to 2000.

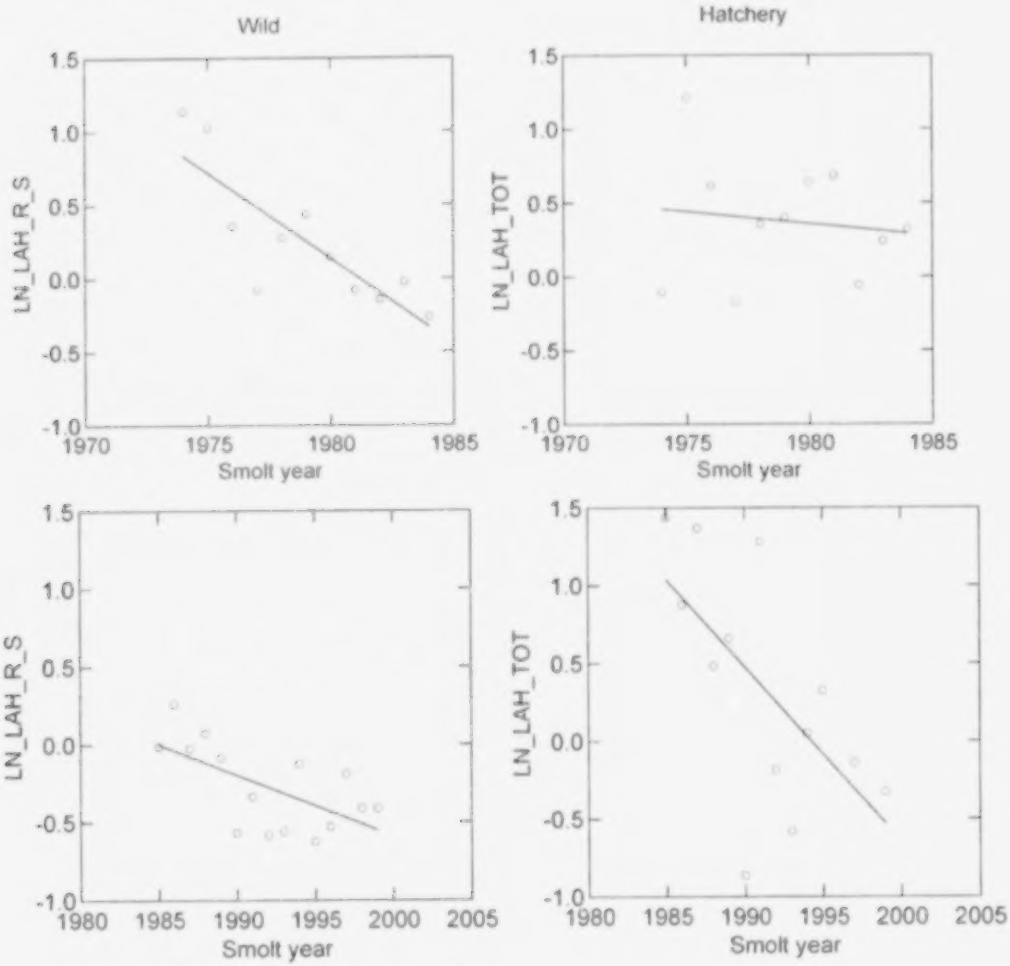

Figure 12. Scatter plot and fitted linear trend lines of Ln(Recruits/Spawner) for wild (left column) and Ln(Smolt to one-sea winter return) hatchery (right column) Atlantic salmon counted at or above Morgans Falls on the LaHave River prior to (top panels) and after (bottom panels) the 1985 Salmon Management Plan, equivalent to the 1982 egg deposition year.

4

ESTIMATION OF MORTALITY FOR ATLANTIC SALMON
(*Salmo salar* L.)

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INTRODUCTION

Anadromous Atlantic salmon (*Salmo salar* L.) occupies two distinct habitats during its lifetime; freshwater and marine. As such, life cycles of Atlantic salmon are frequently described for each distinct aquatic environment. There are numerous estimates of natural mortality (M) for the freshwater stages of Atlantic salmon (see Symons 1979; Chadwick 1987) because the freshwater life stages can be readily monitored and juvenile salmon are not subjected to fishing mortality. Estimates of M during the marine phase are much more difficult to obtain because the adults enumerated back to the river have until recently been exposed to both natural and fishing mortality factors at sea. It is the estimation of natural mortality at sea which is of particular interest for management of fisheries, both marine and freshwater.

In the run-reconstruction models (PFA) for the North American and Northeast Atlantic stock complexes, it was assumed that the natural mortality rate is 1% per month after the first year at sea (ICES 2002). This rate of natural mortality is used to calculate the number of fish immediately after the first winter and prior to the high seas fisheries on two-sea-winter (2SW) salmon. When fisheries remove a high proportion of the stock several months before the animals are destined to return to the rivers, the estimate of the PFA is less sensitive to the assumed natural mortality rate than for fisheries of low intensity. The value of natural mortality assumed for the second year at sea is based on an analysis conducted by Doubleday et al. (1979). Because of the importance of this assumption on the run-reconstruction and on advice related to marine fisheries, a review of measures of M for Atlantic salmon is warranted.

This paper reviews theoretical and empirical methods for estimating M for Atlantic salmon. Theoretical methods are those based on life history characteristics such as lifetime fecundity, maximum age, age at maturity, and inverse-weight associations (Hoenig 1983; Jensen 1996; Lorenzen 1996; Mathews and Buckley 1976). Empirical methods are those based on actual measures of smolts and adult abundance at different life stages. Ricker (1976) provided a comprehensive review of empirical methods for estimating M and more recent refinements to these are discussed.

THEORETICAL METHODS

The theoretical methods can provide indications of integrated lifetime and lifestage specific survival rates. Most of the theoretical methods are based on principles defined across a large number of phyla or a large number of species within a group.

Lifetime fecundity determinants of M

For a population at replacement, the reciprocal of the lifetime fecundity of a female provides a measure of M. That is, at replacement, the average eggs produced during the lifespan of one female is sufficient to produce one female adult spawner. Assuming that the sex ratio of the eggs at fertilization is 50:50, then half of the eggs would be female. Thus, the reciprocal of the average life-time fecundity (in terms of female eggs) is equivalent to the average life-time survival rate:

$$S = (0.5 * \text{Fecundity})^{-1}$$

For example, in a totally semelparous population with an average fecundity per female fish of 5,000 eggs, the integrated survival rate from female eggs to female spawner would be 1 per 2,500 (0.5 * 5000), or 0.04%. The higher the average fecundity, the lower the overall survival rate required to sustain the population (Fig. 1).

For Atlantic salmon, the lifetime survival rate can be partitioned into the freshwater phase and the marine phase. The relationship between egg-to-smolt survival and marine survival required to replace the spawners has a hyperbolic form. A halving of the egg-to-smolt survival requires a doubling of marine survival to generate replacement. The higher the fecundity, the lower the required marine survival for a given egg-to-smolt survival rate (Fig. 2). We would expect most stocks which have persisted and been exposed to fisheries to have the egg-to-smolt and marine survival rates to have been frequently above the replacement lines.

Egg-to-smolt survival rates decrease with increasing egg deposition. Egg-to-smolt survival rates less than 0.5% have been observed in some rivers of eastern Canada, particularly at high egg depositions (Chaput et al. 1998). At an egg-to-smolt survival rate of 0.5%, a population would replace itself if the return rate from smolt to adult back to the river for a 1SW stock (average female fecundity of 3,000 eggs) equaled 13% or for a 2SW stock (average female fecundity of 6,000 eggs) if the return rate of smolt back to the river as 2SW salmon was 6.7% (Table 1). A multi-sea-winter stock that spends 24 months at sea and has an average female fecundity of 6,000 eggs could replace itself at sea mortality rates of almost 11% per month if the freshwater survival was greater than 0.5% (Fig. 2). This monthly rate is assumed to apply equally in all months when the fish is at sea.

M Relative to Longevity

Hoenig (1983) suggests a relatively intuitive premise that the longevity and natural mortality rate in a species should be inversely related since animals from a species with a high mortality would not be expected to reach an old age. Using a data set of 134 species (84 fish species) with longevity and natural mortality rate estimates, Hoenig (1983) described mortality (Z as annual instantaneous mortality rate) relative to maximum age (t_{max}) as:

$$\ln(Z) = a + b \ln(t_{max})$$

with $a = 1.46$, and

$b = -1.01$

The maximum age of Atlantic salmon (age at first spawning) varies between 2 and 12 years; marine ages varying from one-sea-winter to five-sea-winters (in Finland) and smolt ages varying from 1 to 7+ years. For a population of Atlantic salmon with a mean smolt age of 2 years and a mean sea age of 2 years, the annual Z would be 1.06 (annual mortality rate of 65%) (Table 2).

At least to the age of first spawning, we would expect a species like Atlantic salmon with its relatively short life span to have high annual natural mortality rates of 34% to 88% per year (3% to 16% per month), integrated over its lifespan (egg to spawning adult).

Beverton and Holt Life History Invariants

Species evolve such that age at maturity occurs when the fecundity function is a maximum (Jensen 1996). Jensen (1996) showed how three special relations called Beverton and Holt life history invariants could be derived from maximization of the fecundity function that optimizes the trade-off between survival and fecundity. One of those invariants has the form:

$$M * x_m = C1$$

where

M = instantaneous natural mortality

x_m = mean age at maturity

$C1$ = constant (1.65; 2.0).

The value of the constant obtained from regression across species agreed well with the theoretical values of the constants (Jensen 1996).

By inputting mean age at maturity of an Atlantic salmon stock, estimates of M can be obtained. Mean age at maturity is the sum of the average smolt age and the average sea age. The theoretical M values for a series of mean ages at maturity are summarized in Table 3. For Atlantic salmon, the mean age at maturity and the longevity are almost synonymous since many populations are highly semelparous. The Beverton-Holt life history invariant mortality rate values are less than those from the longevity association (Table 2, 3) but are still in the range of 24% to 42% per year for the most frequently encountered ages at maturity (3 to 6 years).

INVERSE WEIGHT METHODS

In a multitude of species, mortality rate is considered to be an allometric function of body weight (Ricker 1976) of the form:

$$M = c\,W^x$$

where

M = mortality rate

W = body weight

c = initial mortality rate for fish of unit weight

x = dimensionless exponent

Steady-state principles were invoked to support the allometric weight to mortality relationship. Specifically, in a steady-state system, mortality is the fraction of the annual production in excess of that required to maintain a stable population biomass (McGurk 1986). Estimates of production to biomass ratios for aquatic invertebrates provided a weight exponent of -0.37 (McGurk 1986). Additionally, it was suggested that in a steady-state system, the rate of increase must be balanced by losses such that the mortality rate should decrease with weight to a power of -0.26 to -0.275 (for dry weight) (McGurk 1986).

There are two levels of approximation of the parameters of the inverse-weight relationship: across phyla (holistic approximations) and within a species group.

Holistic approximations

When considered across phyla (from pelagic invertebrates to whales; Ursin 1967; Peterson and Wroblewski 1984; McGurk 1986), there is a negative association between mortality rate and body weight (dry weight) with the exponent (x in equation 4) in the order of –0.25 (McGurk 1986). Using juvenile and adult fish only, Furnell and Brett (1986) reported a wet weight exponent of –0.37. Lorenzen (1996) reported an overall wet weight exponent for fish in natural environments of –0.288 on average, ranging from –0.291 to –0.305 for lake to ocean specific environments. McGurk (1996) references several studies indicating that the weight exponent of mortality of fishes falls within the range of -0.25 to -0.40. Dickie et al. (1987) proposed that over an entire ecosystem, the mortality exponent was about –0.18 and due mainly to metabolic processes but for individual species, the exponent was about –0.37 and determined by ecological factors (relative sizes of prey and predators).

The mortality at unit weight constant (c in equation 4) has been less precisely estimated. McGurk (1986) estimated c at 0.00526 (d^{-1}) or about 1.9 ($year^{-1}$). Lorenzen (1996) provided estimates of c for fish in natural environments which averaged 3.00 ($year^{-1}$) and ranging from 2.53 to 3.69 ($year^{-1}$) for lake to ocean specific environments. For salmonids specifically, c varied between 1.5 and 2.5 (from Fig. 4 in Lorenzen 1996). McGurk (1996) does not provide estimates of c for Pacific salmon but indicates that the daily instantaneous mortality at unit weight was about 53% of the instantaneous daily growth rate.

Variations in the parameters of the allometric equation have differing consequences to the estimates of mortality. Specifically an increase in x (dimensonless exponent) results in a decrease in M. An increase in c (the mortality at unit weight constant) results in an increase in M. A 10% increase in x results in a greater relative decrease in M for increasing body weight. In contrast, a 10% increase in c results in an increase in M of the same relative magnitude for all values of body weight.

Based on data from 113 species/stocks for the ocean environment, Lorenzen (1996) derived the following parameter values (and 90% confidence limits):

c = 3.69 (2.84 to 4.49) (equivalent to M_u in Lorenzen 1996), and

x = -0.305 (-0.351 to –0.257) (equivalent to b in Lorenzen 1996)

Using these parameter values and measures of weight at age of 1SW salmon and 2SW salmon returning to the Miramichi River during 1971 to 1990, the monthly mortality rate during the second year at sea was estimated to be about 2.6% per month (instantaneous monthly rate = 0.027) (Fig. 3). Using the solutions for natural ecosystems (as opposed to aquaculture systems) based on 308 species/data sets (Lorenzen 1996; x = -0.288; c = 3.00), the average monthly mortality rate for Miramichi salmon was 2.5%.

Direct estimates

Estimates of the inverse-weight coefficients can be obtained by combining the allometric model of growth over time with the allometric model of mortality over weight (Mathews and Buckley 1976; Doubleday et al. 1979; McGurk 1996). Specifically, a model is developed which integrates over time such that age and size (weight) can be interchanged. There are two slightly different models for growth presented in the literature; growth as an exponential function of time (Mathews and Buckley 1976) and growth as a power function of time (McGurk 1996). Both approaches are described below.

Growth in salmonids has frequently been modelled using the exponential function (Mathews and Buckley 1976; Doubleday et al. 1979).

$W_t = a e^{gt}$ (Mathews and Buckley 1976, eq. 1; Doubleday et al. 1979)

After assuming that M was inversely related to weight, Mathews and Buckley (1976) defined the following relationship:

$$M_t = c / (a\, e^{gt})$$

$$= k\, e^{-gt} \qquad \text{(Mathews and Buckley 1976; Eq. 2)}$$

where $k = c/a$

The decline in abundance over time follows:

$$dN/dt = -M_t\, N_t$$

Combined with the previous expression for M_t, Mathews and Buckley (1976) integrated the function over the time period of interest (smolt to returning adult) to produce the following:

$$N_t = N_0 e^{\left[{}^{k}\!/_{g} \cdot \left(e^{-gt} - 1\right)\right]}$$

which is the standard survival function:

$$N_t = N_0\, e^{-Z}$$

with $-Z = [k/g\, (e^{-gt} - 1)]$

Taking the logarithm of measured survival results in:

$$\mathrm{Ln}(N_t/N_0) = -Z = k/g\, (e^{-gt} - 1) \text{ and}$$

$$Z = -[\, k/g\, (e^{-gt} - 1)] = k/g\, (1 - e^{-gt})$$

In the absence of fishing mortality, $M = Z$.

Using measures of survival rate from smolt to adult and substituting g from the exponential growth function, a solution for k is derived and it can then be used to estimate M based on growth. Mathews and Buckley (1976) reconstructed survivors from returns to rivers and from catches at several stages during the year at sea. They also indicated that the approach could be extended to situations where fish mature at more than one age.

Alternatively, McGurk (1996) described growth over time as a power function. Over short periods of time, relative growth in weight can be considered constant.

$$\frac{dW}{dt} = GW \qquad \text{(McGurk 1996; Eq. 1)}$$

Over longer periods of time, the relative growth rate decreases allometrically with increasing weight:

$$G_t = aW_t^{-b}$$

Combining the two equations results in the following:

$$\frac{dW}{dt} = aW_t^{1-b} \qquad \text{(McGurk 1996; Eq. 2)}$$

which integrates over time to produce the power function of growth in weight over time:

$$W_t = \left(W_0^{b} + abt\right)^{1/b} \qquad \text{(McGurk 1996; Eq. 3)}$$

As with Mathews and Buckley (1976), McGurk assumed an inverse weight function for mortality ($M = cW^{-x}$). Substituting the equation for W_t into the inverse weight function and subsequently into the rate of decline function ($dN/dt = -M_t\, N_t$), and integrating over the period of interest (usually from smolt emigration set at $t = 0$ to adult returns at time t) produces the following relationship between survival and weight.

$$Ln\left(\frac{N_t}{N_0}\right) = -\left(\frac{\alpha}{\beta}\right)\left(W^{\beta} - W_0^{\beta}\right)$$

where α = c/a (from growth function and inverse weight function parameters)

β = b – x (from growth and inverse weight functions).

McGurk (1996) used Pacific salmon data to test two hypotheses:

1) β not significantly different from 0 because $b \approx x \approx 0.37$ (exponent in the inverse weight mortality function)
2) α was less than 1 because the initial mortality rate (c) is less than the initial growth rate (a).

McGurk's main conclusion was that the Pacific salmon species share the same allometric functions of growth and mortality but differ in smolt and adult body sizes. The mortality weight function was of the form:

$$M = 0.528\ \alpha\ W^{-0.37}$$

i.e. initial mortality rate is 52.8% of the initial growth rate.

He cautions however that the survival-weight relationships cannot be applied without qualification to salmon populations in general or even to brood years within specific populations, annual mortality functions being conditioned by variations in annual body size and growth rates.

Doubleday et al. (1979)

Preliminary estimates of M for Atlantic salmon during the second year at sea were presented by Doubleday et al. (1979) based on the approach of Mathews and Buckley (1976). The values reported by Doubleday et al. (1979) have been used in the run-reconstruction models for both North American and European stocks of Atlantic salmon.

The paper addressed two issues:

1) testing the inverse-weight hypothesis for Atlantic salmon, and
2) estimating M in the second year at sea based on the inverse weight hypothesis.

It was assumed that the growth in weight function was independent of smolt size. If mortality is an inverse function of weight, then the integrated mortality (M_{INT}) on smolts to reach a given weight can be calculated from:

$$M_{INT} = \int_0^t M(t)dt$$ with t in units of time (days, months, …)

$$= \int_0^{tw} \frac{K}{W(t)}dt$$ because M(t) = K / W(t)(inverse-weight function)

The allometric growth function was used to model growth in weight.

$$W(t) = A\ e^{gt}$$

By letting t = 0 be the time of smolt entry to the ocean, then W(0) = A (because $e^{g0} = 1$), i.e. A in the equation is the average weight of smolts going to sea (W_0).

Combining the allometric growth function with the inverse weight function results in the same equation defined by Mathews and Buckley (1976):

$$M_t \quad = \quad \frac{K}{Ae^{gt}}$$

$$\quad = \quad \frac{K}{A}e^{-gt}$$

Since we have A = W_0 (i.e. weight of smolts going to sea), then the integrated mortality to a time t is written:

$$M_{INT} \quad = \quad \int_0^t \frac{Ke^{-gt}}{W_0}dt$$

$$\quad = \quad \left[\frac{Kg}{W_0}\left(1-e^{-gt}\right)\right]_0^t$$

Doubleday et al. (1979) suggested that the greatest mortality occurred in the initial stages when the fish were small compared with later in life (after one year at sea) when the fish were much larger. This is consistent with the inverse-weight hypothesis that M ~ c / W. Since smolts are about 1% the weight of salmon after one year at sea (20-40 g versus 2000 – 4000 g), then variations in integrated mortality would be defined by smolt size. The further assumption made was that beyond the arbitrary size, which they set at 500 g, the integrated mortality rate was equal for different smolt sizes. This means that all the variations observed in sea mortality are due to the effects on smolt size expressed before they reach the arbitrary weight of 500 g. If this is true, then there should be a linear relationship between the integrated mortality over the entire life at sea and M_{INT} for smolts from time at river entry to time when they reach 500 g.

M_{INT} for smolts up to 500 grams weight equals:

$$M_{INT} \quad = \quad \int_0^t \frac{Ke^{-gt}}{W_0}dt \qquad \text{where t = time for smolts to reach a weight of 500 g}$$

$$\quad = \quad \left[\frac{Kg}{W_0}\left(1-e^{-gt}\right)\right]_0^t$$

$$\quad = \quad \frac{Kg}{W_0}\left(1-\frac{W_0}{500}\right)$$

Letting

$$X \quad = \quad \frac{1}{W_0}\left(1-\frac{W_0}{500}\right) \qquad \text{(X is a variable describing smolt size),}$$

and since

$$Ln(N_t/N_0) \quad = \quad Ln(S) \quad = \quad -M_{INT}$$

then if the inverse-weight hypothesis is appropriate, Ln(S) should be a linear function of X with a slope equal to -K*g.

Using data from the River Bush representing three years with two smolt groups (1, 2 years) of survival data to the one-sea-winter stage, Doubleday et al. (1979) indicated that there was a negative slope at a 10% significance level ($p = 0.16$; Fig. 4). They make a case for excluding the age-2 smolt data of the 1975 cohort because of a furunculosis outbreak and when that point is excluded, the negative slope has a significance level of 0.025 ($p = 0.021$). It should be noted that a plot of smolt size against survival data provided the same evidence of survival being conditioned by smolt size (or initial growth).

Having demonstrated some support for the inverse-weight hypothesis, Doubleday et al. (1979) proceeded to estimate M_{INT} for intervals of time at sea. They used data from the River Bush (N. Ireland, U.K.; same data as in the inverse-weight hypothesis test) and data from the Sandhill River (Labrador, Canada).

To do the analysis, the growth in weight function must first be defined which then allows the estimation of the proportionality factor (K) in the inverse weight function, and mortality rates at different periods of time in the ocean, conditioned by weight.

The age and growth data for the River Bush fish are from Table 4 in Doubleday et al. (1979) and reproduced in Figure 5 (this paper). The weight at release data published in Table 4 of Doubleday et al. (1979) are inappropriately labelled as g units when they are in 0.1 g units. All smolt weights are considered to be at day = 0. The parameters of the exponential growth function reported in Doubleday et al. (1979) are identical to those calculated in Figure 5. Doubleday et al. (1979) state that the exponential growth curve seems to be an adequate descriptor of growth from smolts to grilse but overestimates the growth for salmon. Actually, the fit to grilse is not very good either and certainly the exponential function is a poor descriptor of these weight at age data. The linear function is an equally if not more representative descriptor of growth in weight (Fig. 5).

The growth data used for the Sandhill River model is taken from Allen et al. (1972) (Table 5 in Doubleday et al. 1979). Like the River Bush data, the exponential model is not a very satisfactory adjustment to the empirical data, underestimating the weight after one-year at sea and overestimating weight in the second year (Fig. 5). A linear function captures the position of the anchor points in the weight at age.

Assuming an identical mortality function for salmon at the various stages at sea, Doubleday et al. (1979) proposed to estimate cumulative M_{INT} at different stages of ocean life. This is done by estimating the cumulative mortality on smolts of a given destiny which would have produced the observed catch under the constraint that M was a constant inverse-weight function with weight described by a constant growth function. A smolt destiny in this case refers only to the state of the salmon when it is observed (either as a catch or count in the river).

Specifically Doubleday et al. (1979) used the following formulation to estimate the cumulative mortality:

$$N = R_1 e^{\int_0^{t_1} M_t dt} + R_2 e^{\int_0^{t_2} M_t dt} + \ldots$$ [equation (4) in Doubleday et al. (1979)]

where

N = total number of smolts going to sea

$R_1, R_2, \ldots$ = total fishing removals at ages $t_1, t_2, \ldots$

$\int_0^t M_t dt$ = integrated natural mortality rate from t = 0 to t = 1, 2, …

This is similar to the Maturity Schedule model described later where the number of smolts of described destinies are determined based on total numbers of fish at those destinies. In the case of the Doubleday et al. (1979) method, the destinies are not ages at maturity but fishing losses (all) at given ages. For example, a fishery on 1SW salmon at sea removes N' fish from a given river therefore the number of smolts which generated those N' catches (they were destined to be caught at that age) is N' * $e^{(M)}$ (where M is the integrated mortality rate from smolt entry at sea to the time of capture at sea).

Under the assumption that M is an inverse function of W, then the equation can be written:

$$N = R_1 e^{\int_0^{t_1} \frac{K}{W_t} dt} + R_2 e^{\int_0^{t_2} \frac{K}{W_t} dt} + \ldots$$

or

$$N = \sum_{t=t} R_t e^{\int_0^{t} \frac{K}{W_t} dt}$$

Since the weight at time t can be modelled using the exponential growth function, and knowing N and observations R_t, then the equation can be solved for K by setting the total predicted smolts to the total number that were counted going to sea. Alternatively, when there are several years of observations, a K for all years can be determined by minimizing the residuals of predicted smolts and observed smolts. These solutions were determined using SOLVER in Excel (Fig. 6).

Doubleday et al. (1979) solved for values of K using data from River Bush (one estimate of K for each smolt age group over three smolt runs) and Sandhill River (three estimates of K using three smolt runs).

Based on the description of the methods and the data in Doubleday et al. (1979), the results could be replicated using the Excel formulation.

Using the exponential growth model, the monthly mortality rates for River Bush fish in the second year at sea (days 516 to 834) ranged between 0.1% and 0.3% per month with survival of age-1 smolts less than that of age-2 smolts (Table 4). For the Sandhill River salmon, mortality rates in the second year at sea (months 14 to 24) ranged between 1.2% and 1.5% per month (Table 4). The growth rates of Sandhill River fish were modelled as being lower than those of River Bush with the end result that mortality rates on Sandhill River fish were higher (Fig. 5).

The exponential growth function is not a very satisfactory representation of the weight at age of salmon at sea (Fig. 5). For both stocks, weight at age of 1SW salmon is underestimated while that of 2SW salmon is overestimated (excessively so for River Bush). Doubleday et al. (1979) identified this as an issue and indicated that mortality rates derived using the exponential model were minimum. They analysed an alternative model for growth of Sandhill River fish ($W(t) = a\ e^{[bt2 + ct]}$) and concluded based on lower mortality rates estimated with this alternative model that the use of the exponential model did not greatly affect the results (Doubleday et al. 1979; p. 12).

Simpler linear growth models were adjusted to the data from River Bush and North America (Fig. 5). When these models were applied to the life stage recovery data, the mortality rate estimates in the second year at sea increased slightly to between 1.4% and 1.7% for the Sandhill River salmon. There was a greater increase for the River Bush fish, to between 0.8% and 1.8% (Table 4) resulting from the lower weight at age predicted for fish of age 834 days.

DIRECT ESTIMATES OF SEA MORTALITY FROM SMOLT COUNTS

There are a number of rivers on both sides of the Northwest Atlantic with estimates of sea survival back to the river. Ritter (1989) reviewed the literature on survival of salmon at sea and concluded that sea survivals were stock dependent with average sea survivals for North American populations to the first sea winter of 10% to 20% per year. The sea survivals of European stocks are generally higher with survival rates to the coast of River Bush smolts in the order of 35% (Crozier and Kennedy 1994) and survival rates to other rivers generally being greater than 10% (various ICES working group reports). These rates are for 1SW fish. For stocks with multiple ages at return, the values reported are not survival rates but return rates at age. When there are two or more ages at maturity, the ratio of returns at age to total smolts underestimates the survival because fish not returning to the river after one year include those which died and those which are destined to spend additional time at sea. The actual marine survival rates of smolts in each of the age-at-return groups are higher than the return rates. These annual return rates (integrated over the year) do not provide any information on the trajectory of the mortality function.

MATURITY SCHEDULE METHOD

Ricker (1976) summarized a number of approaches which he termed "maturity schedule methods" to derive estimates of natural mortality at sea for stocks which mature at two or more different ages. A particular approach termed "Murphy's Method" (Ricker 1975) was used to estimate the ocean mortality of Icelandic ranched Atlantic salmon during the second year at sea (Jonasson et al. 1994). These methods provide measures of integrated mortality over one-year intervals. As with the other methods, there is no measure of a functional relationship at intervals of less than one year. A variation of these methods which allows estimates of survival during the first and second years at sea is described by Chaput et al. (2003) and summarized below.

The model proposed by Chaput et al. (2003) allows for the estimation of survival rates during the first and second years at sea based on return of 1SW and 2SW salmon and sex ratios of outmigrating smolts. The model makes some general assumptions:

1) Survival rates at age for males and females are similar,
2) Survival rates in the first year at sea of maturing and non-maturing salmon are similar, and
3) Maturity schedules differ between males and females.

Given the observed returns back to the river of male and female salmon at sea-age, we can infer survival rates during the first year at sea and the second year at sea.

Let:

N_{0M} = number of male smolts leaving the river,

N_{0F} = number of female smolts leaving the river,

N_{1M} = number of male 1SW salmon returning to the river,

N_{1F} = number of female 1SW salmon returning to the river,

N_{2M} = number of male 2SW salmon returning to the river,

N_{2F} = number of female 2SW salmon returning to the river,

M1 = instantaneous mortality rate during the first year at sea, and

M2 = instantaneous mortality rate during the second year at sea.

Then Chaput et al. (2003) show that:

S2 = survival during the second year at sea

= e^{-M2}

= $(N_{0M} * N_{2F} - N_{0F} * N_{2M}) / (N_{0F} * N_{1M} - N_{0M} * N_{1F})$

S1 = survival during the first year at sea

= e^{-M1}

= $(N_{1M} + N_{2M}\, e^{M2}) / N_{0M}$

In the absence of smolt production estimates and therefore survival estimates, S2, can be estimated but not S1.

S2 = $(N_{2F} * \text{Ratio} - N_{2M}) / (N_{1M} - N_{1F} * \text{Ratio})$

where

Ratio = sex ratio of smolts in the sample assumed to represent the smolt run

= N_{0M} / N_{0F}

Chaput et al. (2003) examined the sensitivities of the model to input parameters including sex ratio inputs and violations of the assumptions. They applied the model to data from four rivers in eastern Canada and in this paper, the model is applied to data from the River Scorff (France).

For de la Trinité River (Zone Q7, Quebec), survival rates in the first year declined from a high of about 6% to recent low values of 2% to 3%. Survival rates in the second year improved from a low of 20% to 30% to recent levels of about 50% to 60% (Chaput et al. 2003).

For the Saint John River at Mactaquac hatchery smolts (one year old smolt program), survival in the first year at sea varied between 1.2% and 3.2% while survival in the second year at sea was about 10% with a peak of 25% for the 1993 smolt cohort. Monthly mortality rates for the hatchery stock in the second year at sea were from 10% to 20% with rates nearest the maximum value in recent years (Chaput et al. 2003).

Survival rates during the second year at sea for the Miramichi River were variable and low since 1983 and showed no change resulting from reduced marine exploitation outside the coastal waters (Chaput et al. 2003). Monthly mortality rates were about 10%, twice to four times the levels measured for de la Trinité River stock, indicating that the mortality at sea in the second year for this stock remained high.

For the River Scorff stock of France, survival in the first year at sea was estimated to be slightly better than the survival in the second year, but both were generally less than 15% (Table 5). Monthly mortality rates for the second year at sea for this stock were high at about 16%, and similar to some rates estimated for North America.

CONCLUSIONS ON M

The results of the maturity schedule model and the implications of the inverse-weight model support the widely held view that the major source of mortality in the ocean occurs during the first year. Mortality in the second year at sea is generally lower than in the first year.

A revisit of the Doubleday et al. (1979) paper supports the conclusions of the authors if the exponential growth model is used. However, a simple linear growth model provided a better characterization of the observed sizes at age in the ocean and resulted in monthly mortality rates for River Bush fish which were between 0.9% and 1.8%. For the Sandhill River data, the linear growth model indicated monthly mortality rates in the second year of 1.4 to 1.7%.

The maturity schedule model applied to three stocks in North America indicated that the mortality in the years after 1992 was in the order of 1.5% to 6% per month with 5% being a common estimate for de la Trinité River (Chaput et al. 2003). Estimates on two Maritime multi-sea-winter stocks, indicated that mortality rates in the second year remain high. For the hatchery stock, monthly mortality rates of 15% to 20% were estimated whereas, 10% to 15% monthly mortality rates were frequently estimated in the Miramcihi River wild stock. High mortality rates in the second year at sea have also been estimated for Icelandic stocks (Jonasson et al. 1994; Gudbergsson and Gudjonsson 2003). This suggests an additional issue with the PFA modelling which considers the value of M to be similar for all stocks.

Life history theory models do not contradict the possibility that mortality of salmon at sea, even in the second year can be high. Because of their generally high juvenile (freshwater) survival rates, populations can persist even under high mortality rates at sea. It should be remembered that salmon have unusually high annual mortality rates at sea compared with other marine fish species for which annual mortalities of 18% (M = 0.2) are assumed for many species in contrast to the 65% to 95% mortality observed in Atlantic salmon stocks (Cairns 2003).

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Table 1. Survivals and mortalities for Atlantic salmon at replacement relative to the lifetime fecundity values and freshwater mortality rates.

Age	Survivors at constant M		Egg-to-smolt survivals of 0.5%	
Total eggs	3000	6000	3000	6000
Female progeny				
Eggs	1500	3000	1500	3000
Fry (0.5 yrs)	722	1539		
Parr 1+ (1.5 yrs)	167	405		
Parr 2+ (2.5 yrs)	39	107		
Smolt (3.5 yrs)	9	28	7-8	15
1SW (5 yrs)	1	4	1	
2SW (6 yrs)		1		1
Freshwater – Z (A)	5.12 (99.4%)	4.67 (99.1%)	5.30 (99.5%)	5.30 (99.5%)
Marine – Z (A)	1.46 (77%)	2.67 (93%)	2.01 (87%)	2.71 (93%)
Marine phase only	Lifetime integrated		Anchored by freshwater survival	
All years - Z (A)	2.19 (89%)	3.34 (96%)	2.01 (87%)	2.71 (93%)
Per year – Z (A)	1.46 (77%)	1.33 (74%)	1.34 (74%)	1.08 (66%)
Per month – Z (A)	0.12 (11.5%)	0.11 (10.5%)	0.11 (10.6%)	0.09 (8.6%)
Percent mortality in marine phase	30%	42%	28%	34%

Table 2. Lifetime survival rate based on longevity.

Estimated annual Z over the lifetime of the animal

Mean Smolt Age	Mean sea-age (years)				
	1	2	3	4	5
1	2.14	1.42	1.06	0.85	0.70
2	1.42	1.06	0.85	0.70	0.60
3	1.06	0.85	0.70	0.60	0.53
4	0.85	0.70	0.60	0.53	0.47
5	0.70	0.60	0.53	0.47	0.42

Estimated annual mortality rate (A) over the lifetime of the animal

Mean Smolt Age	Mean sea-age (years)				
	1	2	3	4	5
1	88%	76%	65%	57%	51%
2	76%	65%	57%	51%	45%
3	65%	57%	51%	45%	41%
4	57%	51%	45%	41%	37%
5	51%	45%	41%	37%	34%

Estimated monthly mortality rate (A) over the lifetime of the animal

Mean Smolt Age	Mean sea-age (years)				
	1	2	3	4	5
1	16%	11%	8%	7%	6%
2	11%	8%	7%	6%	5%
3	8%	7%	6%	5%	4%
4	7%	6%	5%	4%	4%
5	6%	5%	4%	4%	3%

Table 3. Estimated mortality rates based on the Beverton-Holt life history invariant of mean age at maturity.

Estimated annual instantaneous mortality rate (Z)

Beverton-Holt invariant	Mean age at maturity (years)						
C1	2	3	4	5	6	7	8
1.65	0.83	0.55	0.41	0.33	0.28	0.24	0.21
2.0	1.00	0.67	0.50	0.40	0.33	0.29	0.25

Estimated annual mortality rate (A)

Beverton-Holt invariant	Mean age at maturity (years)						
C1	2	3	4	5	6	7	8
1.65	56%	42%	34%	28%	24%	21%	19%
2.0	63%	49%	39%	33%	28%	25%	22%

Estimated monthly mortality rate

Beverton-Holt invariant	Mean age at maturity (years)						
C1	2	3	4	5	6	7	8
1.65	6.6%	4.5%	3.4%	2.7%	2.3%	1.9%	1.7%
2.0	8.0%	5.4%	4.1%	3.3%	2.7%	2.4%	2.1%

Table 4. Estimates of mortality rates for Atlantic salmon using the inverse-weight hypothesis applied to data from River Bush (N. Ireland) and Sandhill River (Labrador, Canada) as described by Doubleday et al. (1979). In the table, n.e. means not estimable.

Stock	Growth Model	Age Group	Cohort	Lifetime Survival	Mortality - 2nd Year at Sea	
					2nd Year	Monthly
River Bush	Exponential	Age-1	All three	8.5%	3.4%	0.3%
		Age-2,2+	All three	34.3%	1.5%	0.1%
		Age-1	1974	8.4%	3.4%	0.3%
			1975	13.0%	2.8%	0.3%
			1976	8.5%	3.4%	0.3%
		Age-2,2+	1974	26.8%	1.8%	20.0%
			1975	n.e.	n.e.	n.e.
			1976	24.5%	1.9%	20.0%
	Linear	Age-1	All three	7.3%	17.0%	1.8%
		Age-2,2+	All three	31.9%	7.8%	0.8%
		Age-1	1974	6.7%	17.5%	1.8%
			1975	10.9%	14.6%	1.5%
			1976	8.4%	16.2%	1.7%
		Age-2,2+	1974	24.7%	9.5%	0.9%
			1975	n.e.	n.e.	n.e.
			1976	22.4%	10.1%	1.0%
Sandhill River	Exponential	All ages	1969	15.8%	12.5%	1.3%
			1970	18.3%	11.6%	1.2%
			1971	12.1%	14.2%	1.5%
	Linear	All ages	1969	15.8%	13.8%	1.5%
			1970	18.2%	12.8%	1.4%
			1971	12.0%	15.7%	1.7%

Table 5. Estimates of survival rates at sea during the first and second years for salmon from the River Scorff (France) using the maturity schedule model. Data are courtesy of E. Prevost (INRA France).

River Scorff		Year of Smolt Run			
		1995	1996	1997	1998
Smolts	Male	2402	1260	4046	1902
	Female	3804	2001	6582	2925
1SW Salmon	Male	405	222	357	114
	Female	249	245	170	154
2SW Salmon	Male	12	4	14	9
	Female	63	20	71	48
Annual survival rates					
Year 1		17.4%	18.0%	9.2%	na
Year 2		11.2%	13.1%	12.0%	na
Monthly mortality rates					
Year 1		13.5%	13.3%	18.0%	na
Year 2		16.7%	15.6%	16.2%	na

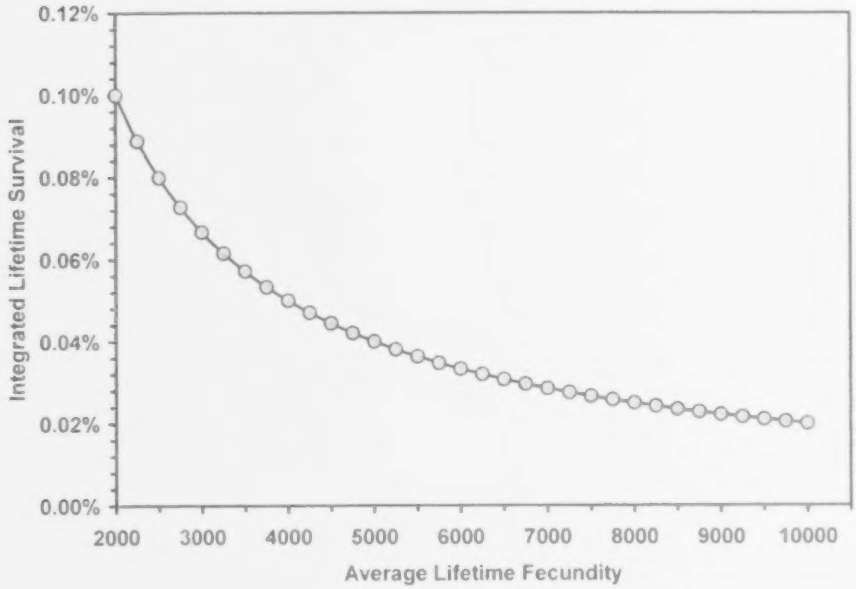


Figure 1. Integrated lifetime survival rate for a population of semelparous Atlantic salmon at replacement relative to the average lifetime fecundity of an individual female.

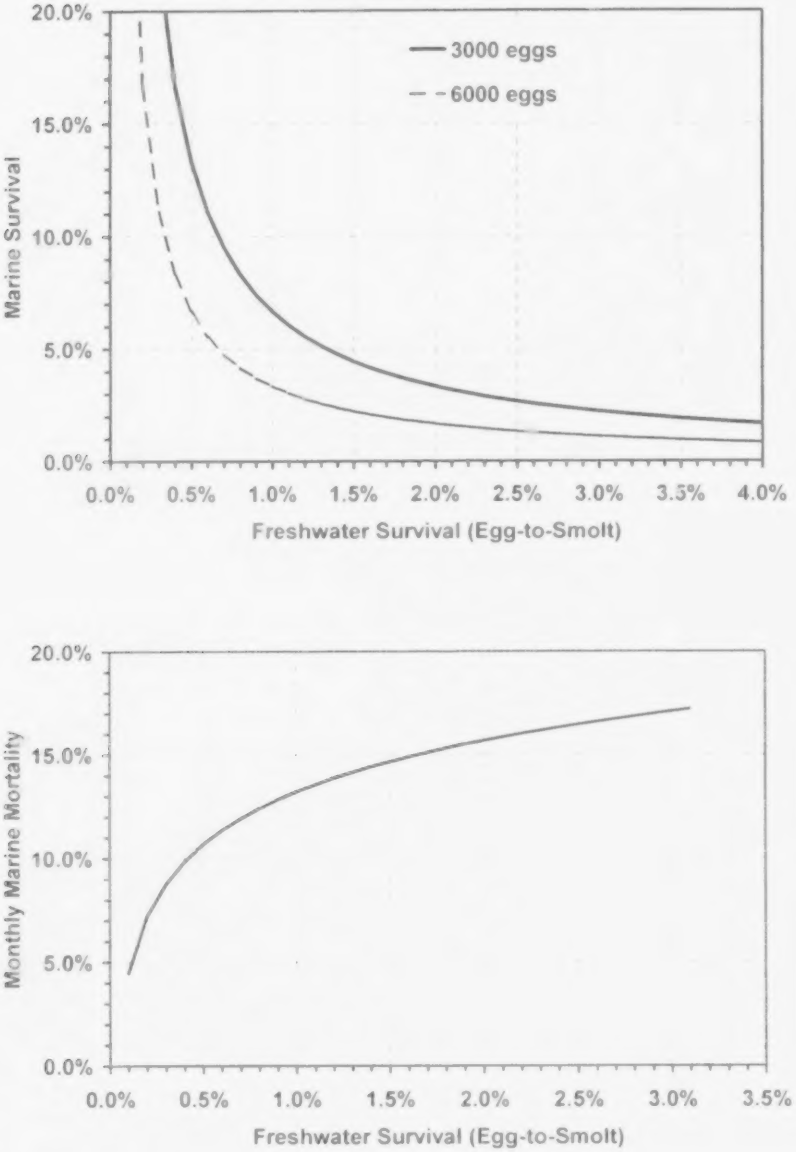


Figure 2. Replacement isopleths defined by the freshwater survival and marine survival axes for two populations of Atlantic salmon with differing average female fecundities. Values of marine survival and freshwater survival above the replacement lines would produce increased abundance whereas values below the replacement lines result in population declines. Bottom panel shows monthly marine mortality rates which would allow a population of salmon with a mean female fecundity of 6,000 eggs to replace itself relative to freshwater survival variation.

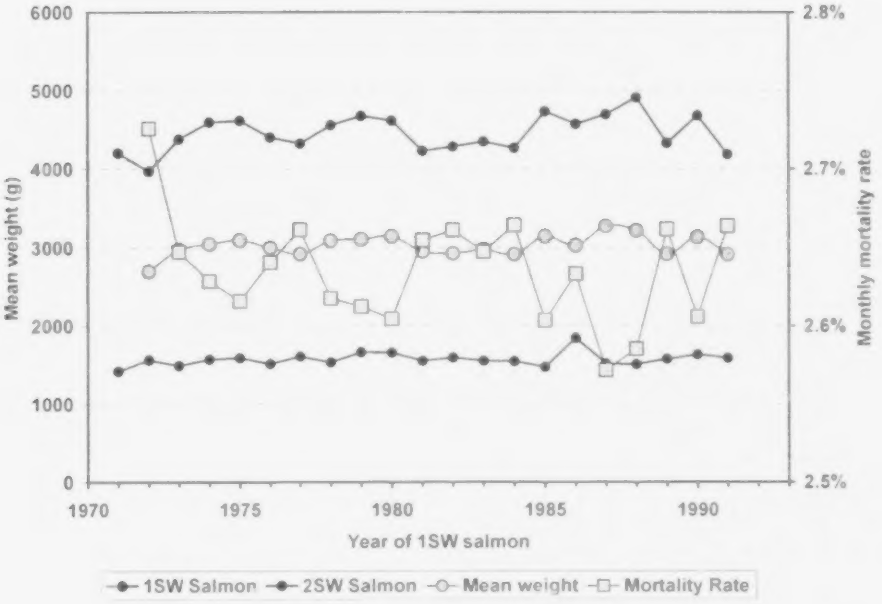


Figure 3. Predicted monthly mortality rate for Atlantic salmon of the Miramichi River in the second year at sea based on the average weight of salmon during the second year at sea and the allometric relationship described by Lorenzen (1996). The average weight during the second year at sea is calculated from the average weight of 1SW salmon sampled in the Miramichi River in smolt year + 1 and the average weight of 2SW salmon sampled in the Miramichi River in smolt year + 2 (Unpublished data). The parameters of the Lorenzen (1996) equation were: $b = -0.305$, $W_u = 3.69$.

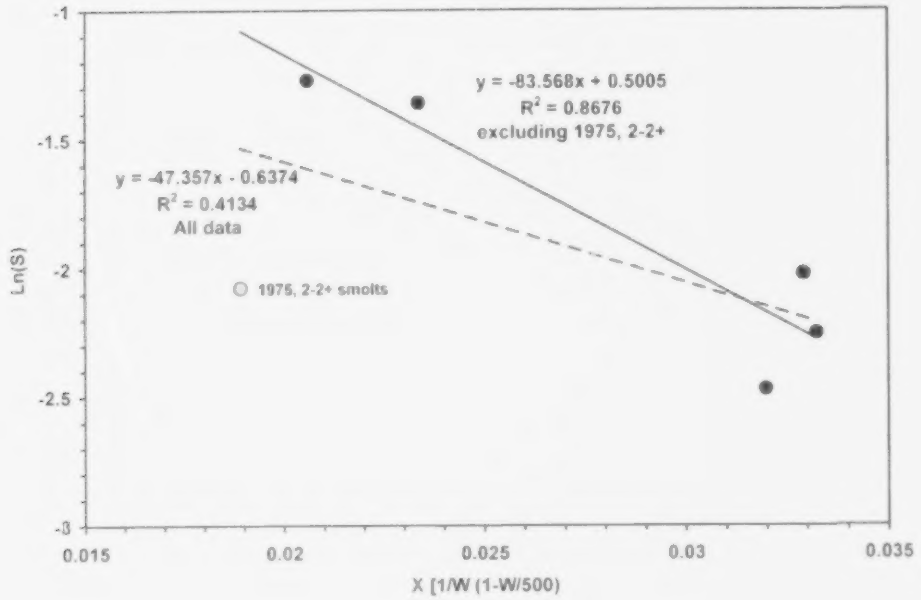


Figure 4. Test of the inverse-weight hypothesis using River Bush data as described by Doubleday et al. (1979). Data are from Table 2 in Doubleday et al. (1979). The regression with all the data has a P-value of 0.16. The regression excluding the 1975 data point has a P-value of 0.021.

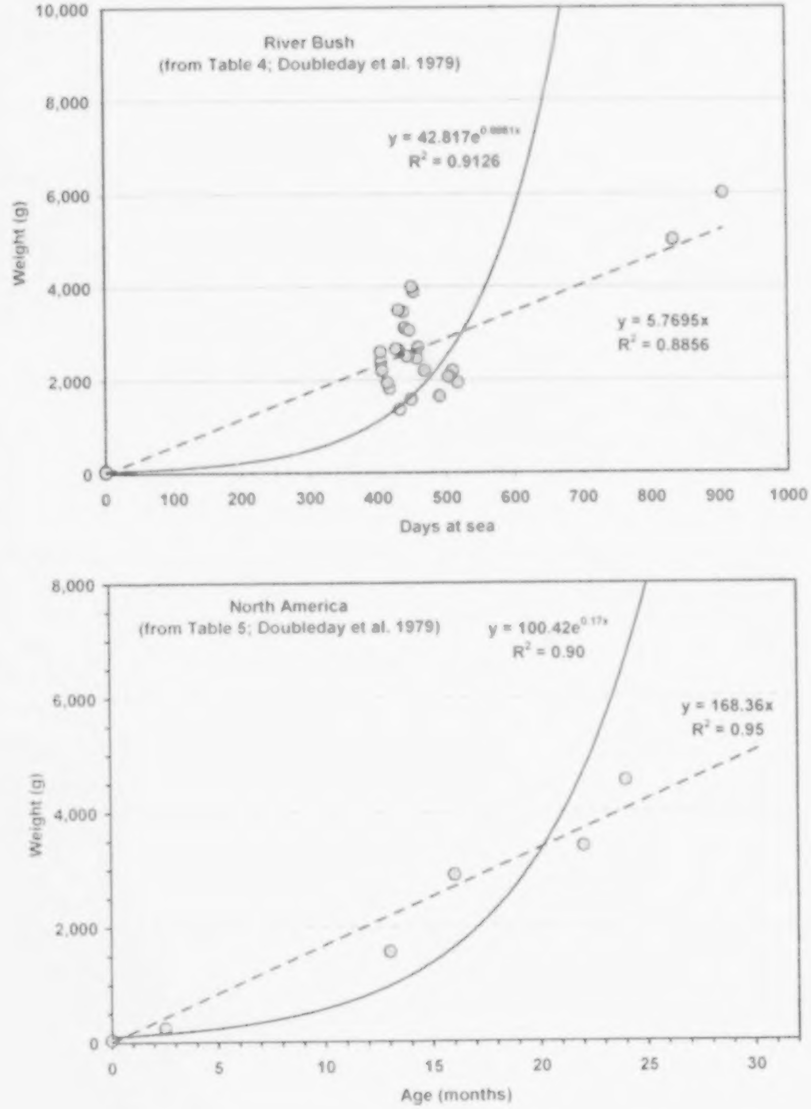
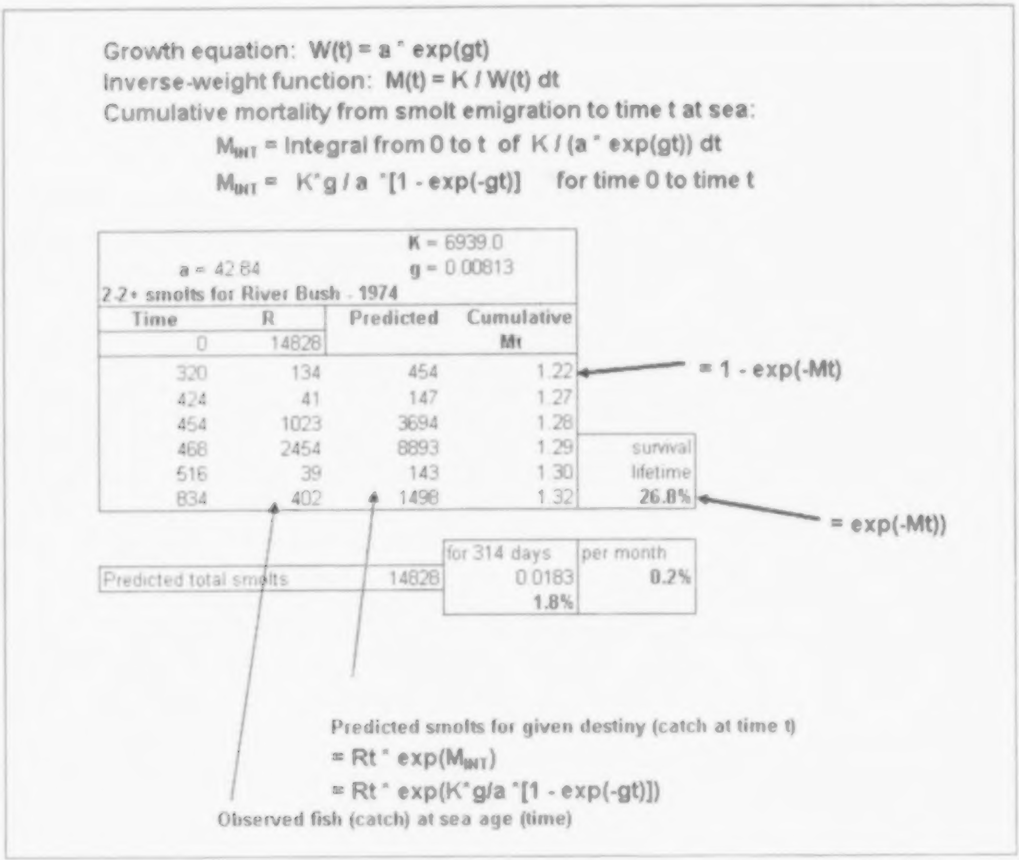


Figure 5. Data from Doubleday et al. (1979) used to parametrize the exponential growth function for salmon from the River Bush (upper panel) and for salmon from North America (lower panel).



Growth equation: W(t) = a * exp(gt)

Inverse-weight function: M(t) = K / W(t) dt

Cumulative mortality from smolt emigration to time t at sea:

M_{INT} = Integral from 0 to t of K / (a * exp(gt)) dt

M_{INT} = K*g / a *[1 - exp(-gt)] for time 0 to time t

K = 6939.0

a = 42.64 g = 0.00813

2.2+ smolts for River Bush - 1974

Time	R	Predicted	Cumulative Mt	
0	14828			
320	134	454	1.22	
424	41	147	1.27	
454	1023	3694	1.28	
468	2454	8893	1.29	survival
516	39	143	1.30	lifetime
834	402	1498	1.32	**26.8%**

= 1 - exp(-Mt)

= exp(-Mt))

		for 314 days	per month
Predicted total smolts	14828	0.0183	**0.2%**
		1.8%	

Predicted smolts for given destiny (catch at time t)

= Rt * exp(M_{INT})

= Rt * exp(K*g/a *[1 - exp(-gt)])

Observed fish (catch) at sea age (time)

Figure 6. Formulation for estimating the mortality at sea using the inverse-weight hypothesis. Data and methods are from Doubleday et al. (1979).

5

ESTIMATES OF SURVIVAL OF ATLANTIC SALMON (*Salmo salar* L.) IN THE FIRST AND SECOND YEARS AT SEA

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INTRODUCTION

Estimates of natural mortality (M) of fish are generally difficult to obtain. For Atlantic salmon (*Salmo salar* L.), there are numerous estimates of M for the freshwater stages estimates of M during the marine phase are much more difficult to obtain. Adults enumerated back to the river are of different ages at maturity and until recently have been exposed to both natural and fishing mortality. There remains some fishing related mortality on Atlantic salmon from eastern Canada resulting from the reduced fishery at West Greenland and from bycatch in legal marine fisheries for other species, such as capelin, herring and mackerel. As a result, any direct measures of sea survival as derived from smolt and adult monitoring programs include an additional component of fishing mortality although very low compared to recent historical levels.

This paper does not address the factors which determine natural mortality at sea but presents a model for estimating survival ($S = e^{-M}$) during the first and second years at sea. Ricker (1976) provides a comprehensive review of the methods proposed for estimating M at sea for Pacific salmon, including approaches, which he termed "maturity schedule methods". A particular approach termed "Murphy's Method" (Ricker 1975) was used to estimate the ocean mortality of Icelandic ranched Atlantic salmon during the second year at sea (Jonasson et al. 1994). A variation of this method described below allows estimation of mortality and therefore S in the first and second years at sea.

MATERIALS AND METHODS

It is possible to estimate the sea survival rates of one sea-winter (1SW) and two sea-winter (2SW) salmon during the first and second years at sea (S1 and S2, respectively) using a simple life history model based on the following assumptions:

1. survival rates for males and females are similar,
2. survival rates in the first year at sea are similar for maturing and non-maturing salmon, and
3. maturity schedules differ between males and females.

Defining the following:

N_{0M} = number of male smolts leaving the river,

N_{0M1} = number of male smolts destined to mature after one year at sea,

N_{0M2} = number of male smolts destined to mature after two years at sea,

N_{1M} = number of male 1SW salmon returning to the river,

N_{2M} = number of male 2SW salmon returning to the river,

M1 = instantaneous mortality rate during the first year at sea, and

M2 = instantaneous mortality rate during the second year at sea,

then

$$N_{1M} = N_{0M1}\, e^{-M1} \qquad (1)$$

$$N_{2M} = N_{0M2}\, e^{-(M1+M2)} \qquad (2)$$

The same equations apply to female smolts (N_{0F}; N_{0F1}; N_{0F2};) and female adults maturing at 1SW (N_{1F}) and maturing at 2SW (N_{2F}).

Since $N_{0M} = N_{0M1} + N_{0M2}$, then

$$N_{0M} \quad = \quad N_{1M}\, e^{M1} + N_{2M}\, e^{(M1 + M2)} \qquad (3)$$

and similarly

$$N_{0F} \quad = \quad N_{1F}\, e^{M1} + N_{2F}\, e^{(M1 + M2)} \qquad (4)$$

Therefore

$$N_{0M}/N_{0F} \quad = \quad (N_{1M} + N_{2M}\, e^{M2}) / (N_{1F} + N_{2F}\, e^{M2})$$

and by algebraic manipulation,

$$S2 \quad = \quad e^{-M2}$$

$$= \quad (N_{0M} * N_{2F} - N_{0F} * N_{2M}) / (N_{0F} * N_{1M} - N_{0M} * N_{1F}) \qquad (5)$$

$$S1 \quad = \quad e^{-M1}$$

$$= \quad (N_{1M} + N_{2M}\, e^{M2}) / N_{0M} \quad \text{or} \qquad (6)$$

$$(N_{1F} + N_{2F}\, e^{M2}) / N_{0F}$$

In the absence of smolt production estimates and therefore survival estimates, we can estimate M_2, but not M_1:

$$N_{0M} \quad = \quad N_{1M}\, e^{M1} + N_{2M}\, e^{(M1 + M2)}$$

$$N_{0F} \quad = \quad N_{1F}\, e^{(M1)} + N_{2F}\, e^{(M1 + M2)}$$

Let Ratio = sex ratio of smolts in the sample, assumed to represent the smolt run

= N_{0M} / N_{0F}

and recalling equations (3) and (4)

$$\text{Ratio} \quad = \quad (N_{1M} + N_{2M}\, e^{M2)}) / (N_{1F} + N_{2F}\, e^{M2)})$$

and by algebraic manipulation

$$S2 \quad = \quad e^{-M2}$$

$$= \quad (N_{2F} * \text{Ratio} - N_{2M}) / (N_{1M} - N_{1F} * \text{Ratio}) \qquad (7)$$

Application of the model

The model was applied to the following data sets (Table 1, 5, 6):

1. de la Trinité River (Québec) wild smolts and resultant 1SW and 2SW returns,
2. Saint John River (NB) 1SW and 2SW hatchery returns resultant of age-1 smolts released from Mactaquac Fish Culture Station, and
3. Miramichi River, (NB) returns of wild 1SW and 2SW salmon.

Sex ratios of the smolts were derived from either sampling on an annual basis (de la Trinité River) or samples from one or a few years (Saint John River, Miramichi River).

We examined the sensitivity of the model to the input data and assumptions using Crystal Ball (Pro) (Decisioneering Ltd.). Simulations were based on smolt runs of 60,000 and 300,000 fish comprised of 40% males. It was assumed that 80% of the male smolts and 20% of the female smolts were destined to return after one year at sea. Returns at age and sex were derived from the annual survival rates in the first year and second years at sea of 0.05 and 0.60, respectively, adjusted to the maturation profiles of the male and female smolts. Two sampling proportions for each of smolts, 1SW salmon and 2SW salmon were considered.

	Smolt run size			
	60,000		300,000	
	Sampling proportions		Sampling proportions	
	Min.	Max.	Min.	Max.
Smolts	0.2%	1.0%	0.2%	0.5%
1SW	5%	20%	5%	20%
2SW	5%	20%	5%	20%

A total of 5,000 simulations were run to generate the distributions of the predicted values and to describe the sensitivity of the solutions to the input parameters. The sensitivity index was the proportion of the total variance of the predicted value attributed to the parameter. The effect of different sampling proportions on the variance of the predicted values was described in terms of the relative width of the 10th - 90th percentile (divided by the median value).

Using data from smolt sampling programs and adult returns, we examine evidence regarding the assumption of independence of mortality rates to sex. Circuli spacing data from scales are used to infer similar survival rates in the first year at sea for maturing and non-maturing 1SW salmon.

RESULTS

Model inputs and sensitivities

The data inputs are the numbers of male and female smolts going to sea, the number of male and female 1SW maiden salmon returning to the river the next year, and the number of male and female 2SW salmon returning to the river two years later. In most cases, the numbers of male and female smolts leaving the river are derived from mark-and-recapture experiments. A sacrificed subsample of the run is used to estimate male and female components. These are therefore subject to measurement error. Similarly, returns of 1SW and 2SW salmon, are either estimated or counted and adjusted into age and sex groups through subsamples of the run. Therefore, the adult data also have a component of measurement error.

Except for the case when one of the life stages (age by sex group) is not represented, i.e. no fish sampled of that group, there is always an analytical solution to the model. Not all solutions are biologically feasible. For example, with some combinations of input data, solutions for S1 and S2 can be greater than 1.0 i.e. survival > 1 for one group and < 0 for another. These conditions occur most frequently for small input values.

Sensitivity to sample size

Generally, the proportion of the adult run sampled is higher than the proportion of the smolt run sampled because the sex of adults can be determined using external characteristics (non-lethally). However, the overall sample size of smolts tends to be larger than for adults (e.g., de la Trinité River, Tables 1, 2).

The simulations indicate that the model appropriately estimates the input parameters of interest (M1, M2, Mat_{male}, Mat_{female}) in both simulated run sizes of smolts (Table 3). The medians equal the simulated input values but the relative variances of the estimates (uncertainty) were greatest for the smaller sample sizes, both within and between simulated run sizes (Table 3). The precision of the estimate for survival in the second year at sea (S2) is poor for the small run size simulation with nonsense values (S2 >= 1.0) in up to 10% of the simulations (Table 4; relative contributions to the variance not estimable). This results from extremely small numbers of male salmon in the 2SW age component and occasionally no male salmon in which case there was no solution to the model. The latter scenario happened on average about 3 out of the 5,000 simulations when only 5% of the 2SW age component was sampled. Relative gains in precision for S2 are greatest for increased sampling effort of the 2SW age component, regardless of run size (Table 3). The most precise estimates were obtained at the highest sampling intensities for all life stages.

The estimates of survival in the first year at sea (S1) are most sensitive to the smolt input data (Table 4). The estimates of survival in the second year at sea (S2) are equally sensitive to the 2SW input data and the smolt input data (Table 4). The estimates of survival are essentially insensitive to the 1SW salmon input data. The relative sensitivities of the parameter results to the smolt and 2SW salmon input data vary with the proportions of the run sampled for each component (Table 4).

Bias associated with using an assumed constant sex ratio

Ideally, the input data are collected on annual basis. In some cases, insufficient numbers of fish may be sampled to provide reliable annual estimates of age and sex composition (see Table 1 for de la Trinité River, smolt year 1998 in particular). The bias associated with using assumed values for some of the parameters was examined by simulating populations using variations in sex ratios for smolts, 1SW and 2SW salmon and fitting the model using assumed values. The simulation parameters are similar to those described above.

For assumed values of smolt sex ratio, the bias is more severe on S2 then S1 but in the same direction for both S1 and S2; when the proportion male is less than assumed, then both S1 and S2 are underestimated and vice versa (Fig. 1). For assumed values of 1SW salmon sex ratio, the bias is most severe for S2 and inversely related to that of S1 (Fig. 1). Even small deviations in the assumed sex ratio of 1SW salmon relative to true resulted in large bias and essentially unusable estimates for S2 (Fig. 1). The large bias on S2 associated with the use of an inappropriate sex ratio of 1SW salmon can generally be avoided. These fish can be well sampled because they can be retained in most angling fisheries and are frequently more abundant in returns than 2SW salmon. The bias on S1 is more severe than on S2 when assumed values for 2SW sex ratio are used (Fig. 1).

Bias of model to assumption of similar survival rates for male and female salmon at sea

The model assumes that the survival rate of male and female smolts at sea are similar. Without this assumption, there is no analytical solution for S1 and S2 because there are more parameters than equations. The bias associated with a violation of this assumption was quantified using the simulation model from above with the exception for M1 and M2 differing between males and females. The parameter estimates were derived by fitting the model under the assumption of similar survival rates.

The bias associated with violations of this assumption are as expected: if female survival rates are less than male survival rates, then S1 is underestimated and S2 is overestimated (Fig. 2). Conversely, if female survival rates are higher than male survival rates, then S1 is overestimated and S2 is underestimated. In both cases, the relative bias is more severe for S2 than for S1.

Size of migrating smolts, condition of migrating smolts, and length of returning adults, provide empirical evidence in support of the assumption of equal survival rates at sea of male and female salmon. Smolt runs from the Northwest Miramichi River were sampled in 1998 to 2000. There were no significant differences in length between male and female smolts in 1998 and 1999, but female smolts age 2 in 2000 were longer ($p = 0.06$) than males of the same age by almost 1 cm. Similarly in 1999, the age- 4 male smolts were longer than the age 4 females but these comprise a very small proportion of the total smolt run (Chaput et al. 2002). Atlantic salmon smolts from the Northwest Miramichi averaged 21 g whole weight (samples only), ranging between 8 and 52 g, over the three years sampled and there were no significant differences ($p > 0.05$) in the predicted weights at length of male versus female smolts in any year (Fig. 3; Chaput et al. 2002).

There were no significant differences in length between male and female adult salmon from the early run (summer) component of the Miramichi River but 1SW and 2SW male salmon were statistically significantly longer than female salmon in the fall run. The differences in length were minor, however, 3% for 1SW salmon and 2% for 2SW salmon. Possible explanations for the longer lengths of males relative to females include morphological differences resulting from the elongation of the head of males relative to females and differences in somatic growth to gonadal development between the sexes. These samples were obtained between 1992 and 1999 and would have been subjected to low intensity size-selective fisheries at Greenland (Moore et al. 1995) and possibly small food fisheries in Labrador.

		Fork length at age, sex, by season	
		Summer	Fall
1SW	Male	55.4	57.8
	Female	54.7	56.3
	Sample size	329	2631
	P-value	0.07	< 0.001
2SW	Male	74.5	77.4
	Female	75.0	75.6
	Sample size	589	3628
	P-value	0.15	< 0.001

Bias of model to assumption of similar survival rates for maturing and non-maturing salmon in the first year at sea

The model also assumes that survival rates in the first year at sea are similar for maturing and non-maturing fish. The bias associated with a violation of this assumption was quantified using the simulation model from above with the exception that M_1 was assumed to be different for fish returning as 1SW relative to fish returning as 2SW. The parameter estimates were derived by fitting the model under the assumption of similar survival rates.

The S1 values are unbiased for the maturing component of the stock, i.e., predicted values of S1 are those of the simulated S1 for the maturing component (Fig. 4). The S1 predictions are biased on the non-maturing component. The S2 values are overestimated when S1 for non-maturing is greater than for maturing and they are underestimated for the opposite relation (Fig. 4). The relative bias is more severe for S2 than S1.

Growth profiles from scale circuli spacing provide an indication that conditions for growth can be similar for maturing and non-maturing components during the first year at sea (defined as the end of the narrow band of circuli spacings). Circuli spacing profiles for three smolt cohorts returning as 1SW and 2SW salmon are indicative of similar growth conditions and by inference potentially similar mortality schedules until at least the age groups diverge in the first half of the second year at sea (Fig. 5).

Estimates of survival rates

de la Trinité River

The input data for Atlantic salmon from Rivière de la Trinité are presented in Table 1. Additionally, model error on the estimated smolt run size was assumed to be equal to a C.V. of 10%. Because of small sample sizes for 2SW salmon between 1989 and 1998, these samples were combined and a common sex ratio for 2SW salmon was applied to those years (11 males, 442 females, 453 fish in total) (Table 1).

Survival rates in the first year (S1) have declined from a high of about 6% to recent low values of 2% to 3% (Fig. 6). Survival rates in the second year (S2) have improved from a low of 20% - 30% to recent levels of about 50% to 60% (Fig. 6). The higher rates in the second year correspond to the period of moratoria on commercial marine salmon fisheries in eastern Canada (1992 to the present). The monthly mortality rates during the second year at sea are presently between 3% and 7% with lower values down to 1% estimated to have occurred for the 1994 and 1996 smolt classes (Fig. 7).

There is an indication that the proportion of the smolt cohort maturing at 1SW of age has increased for both males and females (Fig. 8). For the male smolts, the increase occurred in two steps, a first for the 1985 to 1988 smolt cohorts to about 90% of the cohort and a second higher level of 97% for the 1989 and subsequent smolt cohorts (Fig. 8). For the female smolts, the first increase to 5% occurred in 1986 and lasted into 1994 with a subsequent higher proportion 10% occurring from 1995 to the present (Fig. 8). The reasons for the increased predicted maturation rates at 1SW are unknown but it occurred at the same time as overall abundance of salmon began to decline. It also occurred coincidentally with the fishery closures which may have released the larger 1SW salmon.

Saint John River hatchery smolts

For Saint John River age-1 Mactaquac hatchery smolts , sex ratios were only available for 1989, 1990, 1991. The returns of 1SW and 2SW salmon by sex are presented in Table 5. For the 1991 to 1998 smolt cohorts, survival in the first year at sea has varied between 1.2% and 3.2% while survival in the second year at sea has generally been at about 10% with a peak of 25% for the 1993 smolt cohort (Fig. 9). Monthly mortality rates for the hatchery stock in the second year at sea are from 10% to 20% with rates nearest the maximum value in the recent years (Fig. 10). The maturation profiles indicate about 70% to 90% of the males mature after one year at sea whereas generally less than 4% of the females mature after one year (Fig. 11).

Miramichi River

Returns by age group and sex have been estimated for the Miramichi River since 1971 but returns since 1984 represent abundance of the age groups since the closure of the Maritime coastal marine commercial fisheries (Table 6). There are no estimates of total smolt production for these years but smolt studies initiated in 1998 in the Northwest Miramichi provide an indication of the sex ratio of the smolt runs which were 49% female in 1998, 63% female in 1999 and 58% female in 2000 (Chaput et al. 2002). Estimates of mortality during the second year at sea were obtained using the three point estimates of sex ratio from 1998 to 2000 and ignoring the measurement errors in the adult returns. Survival rates during the second year at sea have been variable and low since 1983 and show no change resulting from reduced marine exploitation outside the coastal waters (Fig. 12). Survival rates are as low as those estimated for the hatchery origin salmon from the Saint John River at Mactaquac (Fig. 11). Monthly mortality rates are about 10%, two to four times the levels measured for the Rivière de la Trinité wild stock. Because the annual sex ratios of the smolts are unknown and the measurement errors in the estimates of adult abundance have been ignored, these estimates of survival rates should be considered as an index of relative survival rates in the second year at sea. However, even at the balanced sex ratio assumption (49% female), survival rates have infrequently been above 40% and generally around 20% (Fig. 12) indicating that the mortality at sea in the second year for this stock remains high. Recovery of post-spawner tagged salmon even in the reduced Greenland fishery suggests that fishing mortality is a likely contributor to lower survival rates in the second year at sea (Chaput et. al 2001).

Among stock comparisons

The survival rates of the Rivière de la Trinité smolts are comparable to the survival rates of the hatchery smolts from the Saint John River at Mactaquac during the recent period and not unlike the survival rates of the wild smolts from the 1SW salmon stock of Conne River (Dempson et al. 2003; Fig. 13). Survival rates were also comparable to those of Western Arm Brook (Dempson et al. 2003) prior to 1992 but have been less than those of the latter since the commercial salmon moratorium introduced in 1992 (Fig. 13). Survival rates during the second year at sea (S2) are now estimated to be substantially greater than those of the hatchery stock of the Saint John River and the Miramichi River wild smolts (Fig. 13). S2 rates were comparable between Rivière de la Trinité and Miramichi prior to the fishery moratoria introduced in 1992.

DISCUSSION

The results of the model support the widely held view that the major source of mortality in the ocean occurs during the first year. Mortality in the second year at sea is generally lower than in the first year but greater than the assumed value of 0.01 per month used in the run-reconstruction model for the North American salmon stock complex (ICES 2001). For one wild multi-sea-winter salmon stock of eastern Canada, monthly mortality rates of 5% (ranging between 2% and 15%) were estimated during the time when essentially all commercial fisheries at sea were closed.

Survival in the first year at sea for these MSW stocks are comparable to some of the survivals measured in 1SW salmon stocks of Newfoundland (Dempson et al. 2003) but substantially below the levels measured in European stocks (Crozier and Kennedy 1994). Increased survival of Rivière de la Trinité salmon in the second year at sea appears to correspond to the period of closure of marine coastal fisheries in eastern Canada but similar responses have not been observed in two other stocks in the Maritimes. Correspondingly, survival in the first year at sea has declined. These declines were observed in other stocks of eastern Canada, primarily stocks in Newfoundland and the hatchery stocks in the Maritimes (Dempson et al. 1998; Marshall et al. 1999) pointing to a larger issue than fisheries.

The estimates of S1 and S2 from this model represent survival rates to the time 1SW fish return to the rivers; this would be during June to October which is more than the 12 months since smolt migration to sea. The S2 rates are closer to a 12 month period. The assumption of similar S1 rates for maturing and non-maturing fish is questionable, particularly since these age groups diverge no later than the start of the second year as maturing fish return to rivers while non-maturing fish migrate to feeding grounds off Greenland. It is possible that mortality on maturing fish near the coast would be different from the mortality in the same months for non-maturing fish in the high seas but this presently cannot be verified. Available data on size and condition of smolts, and size of returning adults was inconclusive in rejecting the assumption of similar survival rates for male and female smolts. It is unlikely that this assumption can be further tested.

The results of the model should be used with caution if annual values for sex composition of smolts and adults are not available. Insufficient sampling of the 2SW component results in unreliable estimates of survival in the second year (S2) although aggregating samples over a number of years and assuming a value for the sex ratio introduces less bias than doing the same for the other two data input series.

Similar estimates of survival rates could be derived for stocks where estimates of smolt production and adult returns with corresponding sex ratio information are collected. Alternatively, estimates of survival in the second year at sea could be obtained for rivers in which adult returns are monitored and samples of smolts for determining the sex ratios are available. This is similar to the approach used by Jonasson et al. (1994) and Gudbergsson and Gudjonsson (2003) for ranched Icelandic stocks.

The model provides estimates of the maturation profiles of male and female smolts and there is a suggestion from de la Trinité River analyses of a larger proportion of the smolts maturing after one year at sea in recent years. This increased proportion corresponds to the increases in size-at-age in the returns of adults to this river (F. Caron, Unpublished data) and also to a time period of reduced abundance of Atlantic salmon throughout eastern Canada. Similar increases in size have been noted for Miramichi salmon (Chaput et al. 2001).

Estimates of inter-stage survival could be obtained for other age groups such as consecutive and alternate post-spawner survival rates in stocks where repeat spawners are an important component of the adult returns. Those types of analyses would provide insight into changes in mortality rates on these larger animals as well as possible changes in reconditioning schedules.

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Table 1. Input data for de la Trinité River for estimating survival in first and second year at sea. Smolt estimates are from mark-and -recapture experiments. Adult returns are counts at a fishway.

Rivière de la Trinité

					Adult return estimates										
	Smolt data				Year + 1				Year + 2						
Smolt	Run size	Smolt sampling			1SW	1SW samples			MSW	age samples			2SW samples		
Year	estimate	male	female	total	count	male	female	total	count	2SW	Other	Total	male	female	total
1984	67,922	105	180	285	1053	107	2	109	621	195	17	212	27	125	152
1985	65,847	14	16	30	1589	353	15	368	558	116	10	126	11	72	83
1986	96,316	83	119	202	1304	305	28	333	813	81	6	87	4	54	58
1987	77,342	85	103	188	1639	331	33	364	466	97	14	111	7	57	64
1988	51,590	98	130	228	1839	269	23	292	530	133	26	159	8	90	98
1989	79,710	136	173	309	1905	425	38	463	516	114	8	122	2	66	68
1990	50,109	70	120	190	1334	169	14	183	612	137	10	147	2	92	94
1991	40,696	60	95	155	577	116	23	139	271	50	7	57	1	36	37
1992	50,664	84	102	186	410	116	9	125	309	27	6	33	0	18	18
1993	85,961	85	180	265	579	115	12	127	671	99	8	107	0	69	69
1994	55,769	60	84	144	348	64	5	69	434	55	8	63	2	37	39
1995	71,679	99	121	220	662	111	19	130	557	35	19	54	1	30	31
1996	60,899	87	106	193	393	101	11	112	385	67	11	78	2	53	55
1997	31,659	85	128	213	524	67	12	79	380	40	5	45	1	31	32
1998	28,725	74	97	171	399	34	5	39	251	12	2	14	0	10	10
1999	56,056	56	81	137	250	23	0	23							
2000	39,510	48	62	110											

Table 2. Percentage of the components sampled for the Atlantic salmon from de la Trinité River.

Percentage of the components sampled

	Smolts for sex ratio	1SW salmon for sex ratio	2SW salmon for age and sex
1984	0.42	10.4	24.5
1985	0.05	23.2	14.9
1986	0.21	25.5	7.1
1987	0.24	22.2	13.7
1988	0.44	15.9	18.5
1989	0.39	24.3	13.2
1990	0.38	13.7	15.4
1991	0.38	24.1	13.7
1992	0.37	30.5	5.8
1993	0.31	21.9	10.3
1994	0.26	19.8	9.0
1995	0.31	19.6	5.6
1996	0.32	28.5	14.3
1997	0.67	15.1	8.4
1998	0.60	9.8	4.0
1999	0.24	9.2	
2000	0.28		

Table 3. Accuracy and precision (% width of the 10-90th percentile relative to median value) of the parameter estimates relative to the percentage of the smolts, 1SW and 2SW fish sampled for smolt run sizes of 300,000 and 60,000 fish. (S1 and S2 are survivals in first and second years at sea, respectively).

Smolt run size = 300,000 fish

				Simulation inputs							
				0.05	0.6	0.8	0.2				
	Percentage of run sampled			Simulation estimates (median)				Relative width of 10-90th percentile			
Scenario	Smolts	1SW	2SW	S1	S2	Mat_{male}	Mat_{female}	S1	S2	Mat_{male}	Mat_{female}
1	0.2%	5.0%	5.0%	0.050	0.590	0.804	0.197	6%	78%	12%	28%
2	0.5%	5.0%	5.0%	0.050	0.592	0.802	0.197	5%	68%	10%	25%
3	0.2%	20.0%	5.0%	0.050	0.589	0.802	0.197	7%	69%	9%	19%
4	0.5%	20.0%	5.0%	0.050	0.588	0.802	0.198	5%	62%	7%	15%
5	0.2%	5.0%	20.0%	0.050	0.595	0.803	0.197	6%	57%	11%	27%
6	0.5%	5.0%	20.0%	0.050	0.593	0.802	0.197	4%	49%	10%	25%
7	0.2%	20.0%	20.0%	0.050	0.593	0.802	0.197	6%	47%	8%	18%
8	0.5%	20.0%	20.0%	0.050	0.591	0.802	0.198	4%	38%	6%	15%

Smolt run size = 60,000 fish

				Simulation inputs							
				0.05	0.6	0.8	0.2				
	Percentage of run sampled			Simulation estimates (median)				Relative width of 10-90th percentile			
Scenario	Smolts	1SW	2SW	S1	S2	Mat_{male}	Mat_{female}	S1	S2	Mat_{male}	Mat_{female}
1	0.2%	5.0%	5.0%	0.051	0.575	0.807	0.195	16%	195%	25%	59%
2	1.0%	5.0%	5.0%	0.050	0.583	0.807	0.196	10%	176%	21%	54%
3	0.2%	20.0%	5.0%	0.050	0.575	0.805	0.197	15%	177%	20%	42%
4	1.0%	20.0%	5.0%	0.050	0.580	0.805	0.198	9%	151%	14%	31%
5	0.2%	5.0%	20.0%	0.051	0.590	0.804	0.197	14%	140%	25%	59%
6	1.0%	5.0%	20.0%	0.050	0.595	0.805	0.196	7%	109%	20%	53%
7	0.2%	20.0%	20.0%	0.050	0.590	0.805	0.196	14%	114%	19%	41%
8	1.0%	20.0%	20.0%	0.050	0.593	0.803	0.197	7%	82%	12%	30%

Table 4. Sensitivity of the S1, S2 and maturation schedule estimates to the input data defined as the relative contribution (%) to the variance of the estimates by the input variables for different sampled percentages of the age components. Missing data indicate sensitivity analysis could not be completed because of small sample size (0 fish in particular age and sex category).

Smolt run size = 300,000 fish

				Relative contributions of input variables to the variance of the predicted values											
				Input data											
	Percentage of run sampled			Smolts sampled				1SW Salmon sampled				2SW Salmon sampled			
Scenario	Smolts	1SW	2SW	S1	S2	Mat_{male}	Mat_{female}	S1	S2	Mat_{male}	Mat_{female}	S1	S2	Mat_{male}	Mat_{female}
1	0.2%	5.0%	5.0%	86.0%	33.5%	52.2%	37.5%	0.0%	16.9%	43.2%	61.0%	14.0%	49.6%	4.7%	1.5%
2	0.5%	5.0%	5.0%	93.0%	55.1%	72.4%	59.7%	0.0%	12.3%	25.1%	39.3%	7.0%	32.6%	2.5%	1.0%
3	0.2%	20.0%	5.0%	84.4%	20.2%	20.4%	12.6%	0.0%	49.4%	77.5%	87.0%	15.5%	30.4%	2.1%	0.4%
4	0.5%	20.0%	5.0%	93.5%	38.6%	38.6%	25.1%	0.1%	36.7%	59.4%	74.7%	6.4%	24.7%	2.0%	0.2%
5	0.2%	5.0%	20.0%	60.1%	11.6%	43.9%	36.3%	0.2%	6.7%	39.3%	58.8%	39.7%	81.7%	16.8%	4.9%
6	0.5%	5.0%	20.0%	79.9%	27.4%	67.0%	59.2%	0.0%	5.9%	22.4%	38.1%	21.1%	66.8%	10.6%	2.7%
7	0.2%	20.0%	20.0%	60.0%	9.3%	18.2%	11.6%	0.0%	24.6%	73.4%	87.1%	40.0%	66.2%	8.3%	1.4%
8	0.5%	20.0%	20.0%	81.3%	25.9%	40.3%	28.2%	0.1%	19.8%	52.1%	71.2%	18.7%	54.3%	7.6%	0.6%

Smolt run size = 60,000 fish

				Relative contributions of input variables to the variance of the predicted values											
				Input data											
	Percentage of run sampled			Smolts sampled				1SW Salmon sampled				2SW Salmon sampled			
Scenario	Smolts	1SW	2SW	S1	S2	Mat_{male}	Mat_{female}	S1	S2	Mat_{male}	Mat_{female}	S1	S2	Mat_{male}	Mat_{female}
1	0.2%	5.0%	5.0%												
2	1.0%	5.0%	5.0%												
3	0.2%	20.0%	5.0%	74.2%	24.9%	66.9%	59.3%	0.1%	5.0%	20.8%	37.5%	25.7%	70.1%	12.3%	3.2%
4	1.0%	20.0%	5.0%												
5	0.2%	5.0%	20.0%	88.4%	38.7%	40.0%	26.1%	3.0%	35.8%	57.3%	73.8%	8.5%	25.5%	2.7%	0.1%
6	1.0%	5.0%	20.0%	71.3%	11.0%	10.7%	5.7%	1.1%	53.4%	86.4%	93.9%	27.7%	35.5%	2.9%	0.3%
7	0.2%	20.0%	20.0%	91.2%	55.2%	72.1%	59.1%	0.6%	12.1%	25.0%	40.1%	8.2%	32.7%	2.8%	0.9%
8	1.0%	20.0%	20.0%	75.1%	18.3%	31.6%	21.6%	0.0%	23.0%	61.0%	77.4%	24.9%	58.7%	7.5%	0.9%

Table 5. Input data to estimate survival rates during the first and second years at sea for age-1 hatchery smolts released from Mactaquac Fish Culture Station on the Saint John River, NB. Adult returns are from sampling at a fishway.

Saint John River at Mactaquac 1-year old hatchery smolts and returns

						Adult return estimates									
	Smolt data					Year + 1					Year + 2				
Smolt		Smolt sampling (1989 to 1991)				1SW	1SW samples				2SW	2SW samples			
Year	Releases	Males	Females	Prop.Male	Total	count	male	female	Prop male	total	count	males	females	prop male	total
1991	178,127	317	387	0.450	704	1310	127	4	0.969	131	223	3	35	0.079	38
1992	204,836	317	387	0.450	704	831	58	0	1.000	58	468	46	44	0.511	90
1993	221,403	317	387	0.450	704	883	133	5	0.964	138	456	20	80	0.200	100
1994	225,037	317	387	0.450	704	1544	260	7	0.974	267	600	19	75	0.202	94
1995	251,759	317	387	0.450	704	2893	228	17	0.931	245	485	23	106	0.178	129
1996	286,400	317	387	0.450	704	1616	293	7	0.977	300	235	14	80	0.149	94
1997	286,485	317	387	0.450	704	2135	472	30	0.940	502	579	45	160	0.220	205
1998	297,012	317	387	0.450	704	1690	316	18	0.946	334	185	6	74	0.075	80
1999	305,073	317	387	0.450	704	1413	345	26	0.930	371					

Table 6. Input data to estimate survival rates during the second year at sea for wild salmon from the Miramichi River, NB. Adult returns are from mark and recapture experiments.

					Returns by age and sex			
Smolt	Returns at age		%female		1SW Salmon		2SW Salmon	
Year	1SW	2SW	1SW	2SW	male	female	male	female
1983	29,827	18,189	0.217	0.627	23,355	6,473	6,785	11,405
1984	60,800	25,116	0.228	0.770	46,938	13,862	5,777	19,339
1985	117,549	15,722	0.213	0.900	92,511	25,038	1,572	14,150
1986	84,816	17,396	0.354	0.903	54,791	30,025	1,687	15,709
1987	121,919	11,308	0.215	0.787	95,706	26,213	2,409	8,899
1988	75,231	17,173	0.220	0.756	58,680	16,551	4,190	12,983
1989	90,533	18,076	0.183	0.831	73,965	16,568	3,055	15,021
1990	60,867	21,502	0.144	0.827	52,102	8,765	3,720	17,782
1991	151,022	22,942	0.090	0.825	137,415	13,607	4,015	18,927
1992	88,800	19,860	0.081	0.795	81,652	7,148	4,071	15,788
1993	54,375	27,441	0.183	0.885	44,441	9,934	3,156	24,285
1994	54,054	16,329	0.231	0.813	41,568	12,486	3,053	13,275
1995	49,184	10,421	0.132	0.789	42,692	6,492	2,199	8,222
1996	23,274	3,844	0.140	0.787	20,016	3,258	819	3,025
1997	33,000	9,112	0.202	0.752	26,334	6,666	2,260	6,852
1998	23,000		0.287					

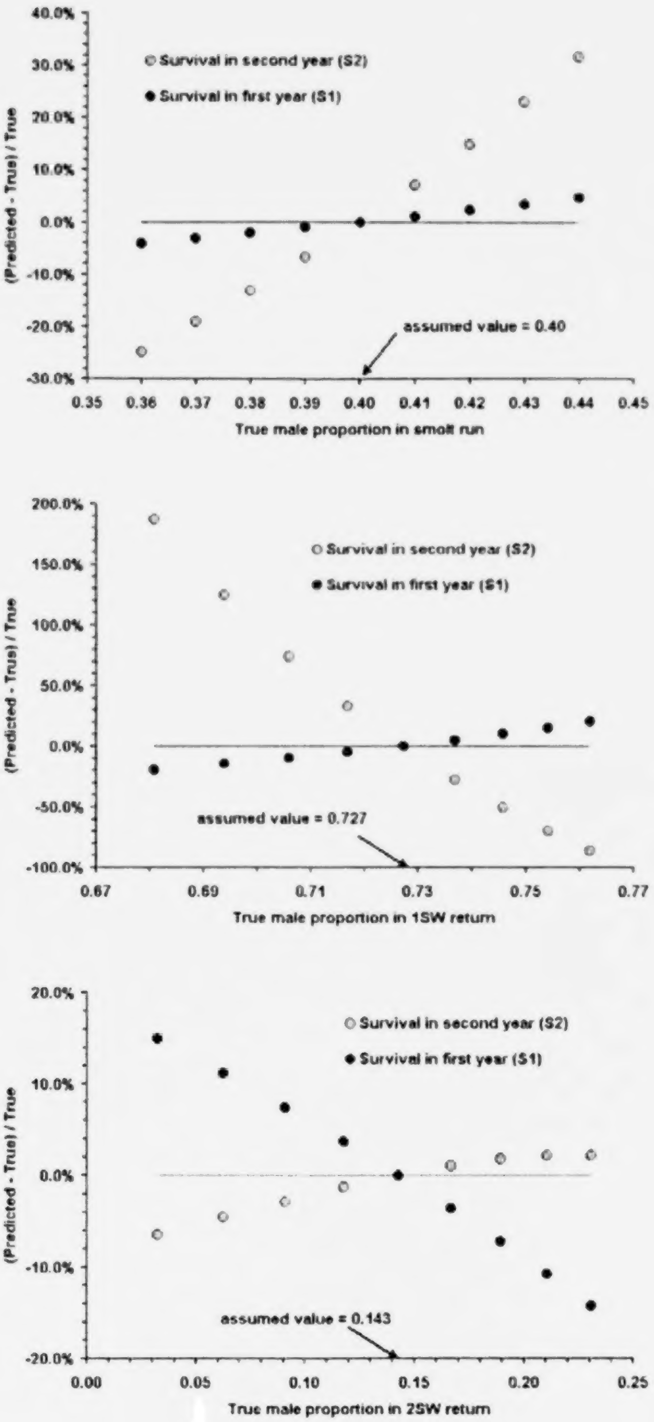


Figure 1. Bias of estimates of S1 and S2 for assumed values of male proportion in smolt run (upper), male proportion in 1SW salmon (middle) and male proportion in 2SW salmon (lower).

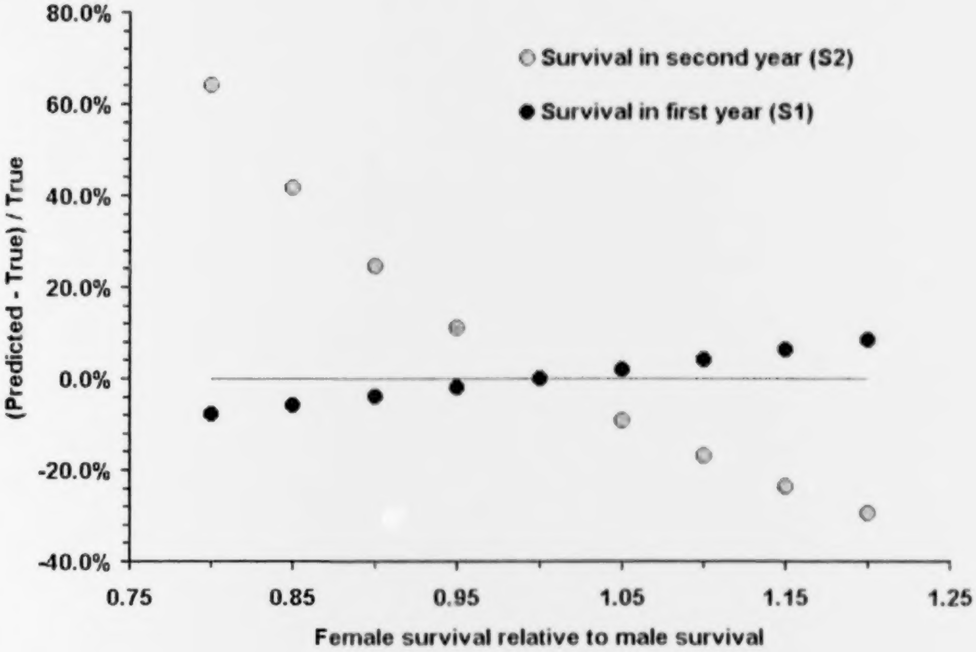


Figure 2. Bias in estimates of S1 and S2 associated with the inappropriate assumption that survivals of male and female salmon are similar.

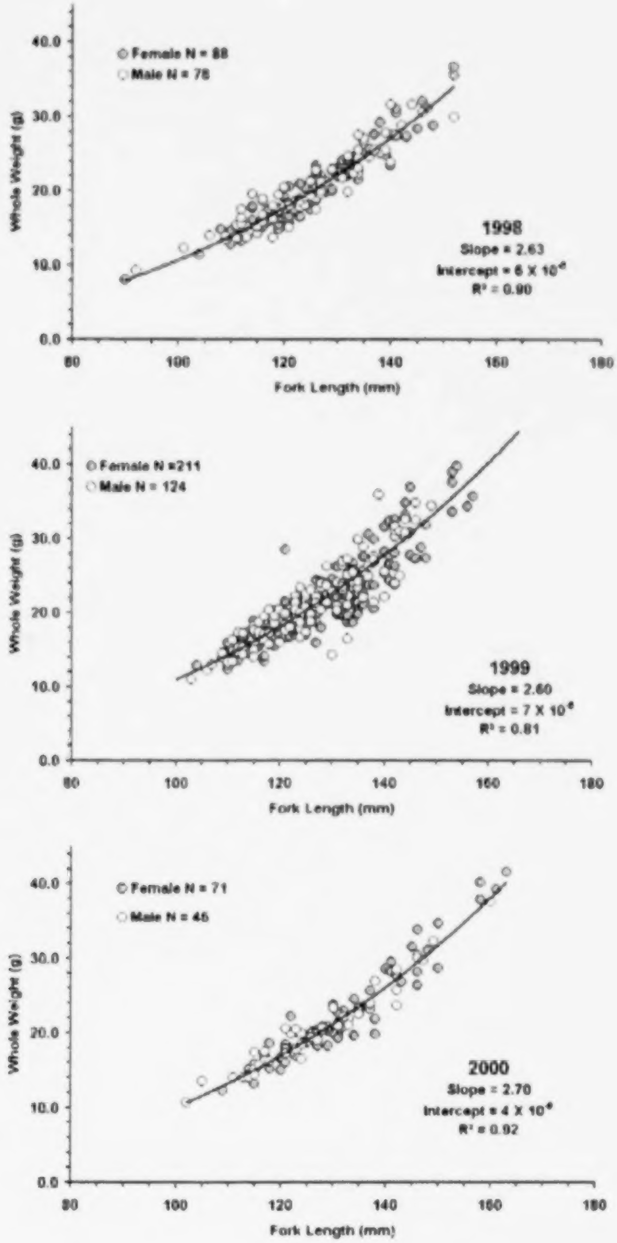


Figure 3. Length weight relationships for wild Atlantic salmon smolts from the Northwest Miramichi River for 1998 (upper), 1999 (middle) and 2000 (lower). The slope and intercept values in each panel are the values of the power function (Weight = intercept * Length ^{slope}) for sexes combined. Data and figures are from Chaput et al. 2002.

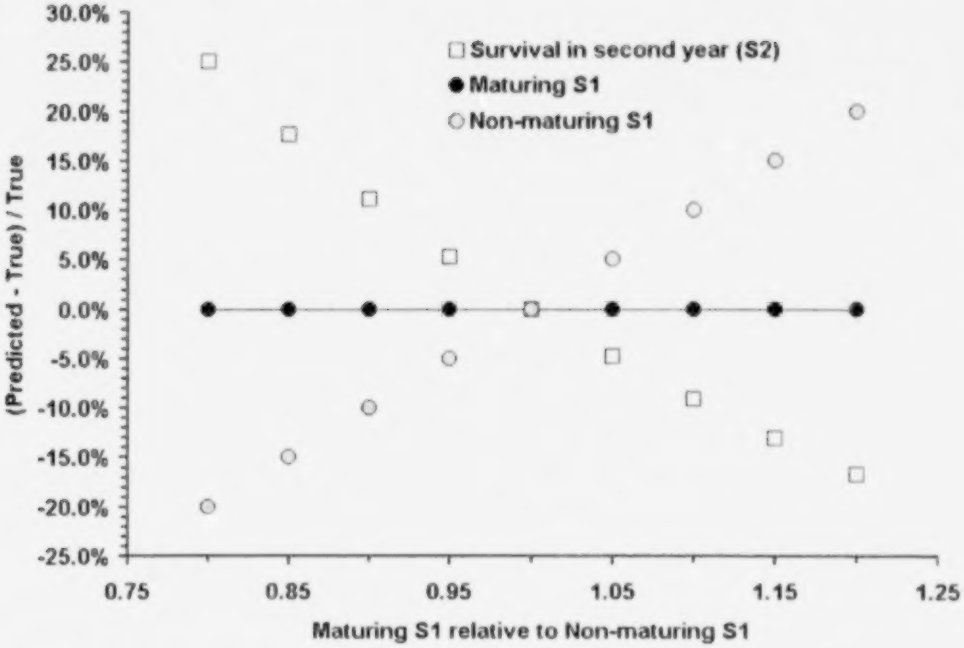


Figure 4. Bias in estimates of S1 and S2 associated with the inappropriate assumption that survivals in first year at sea are similar for maturing and non-maturing components.

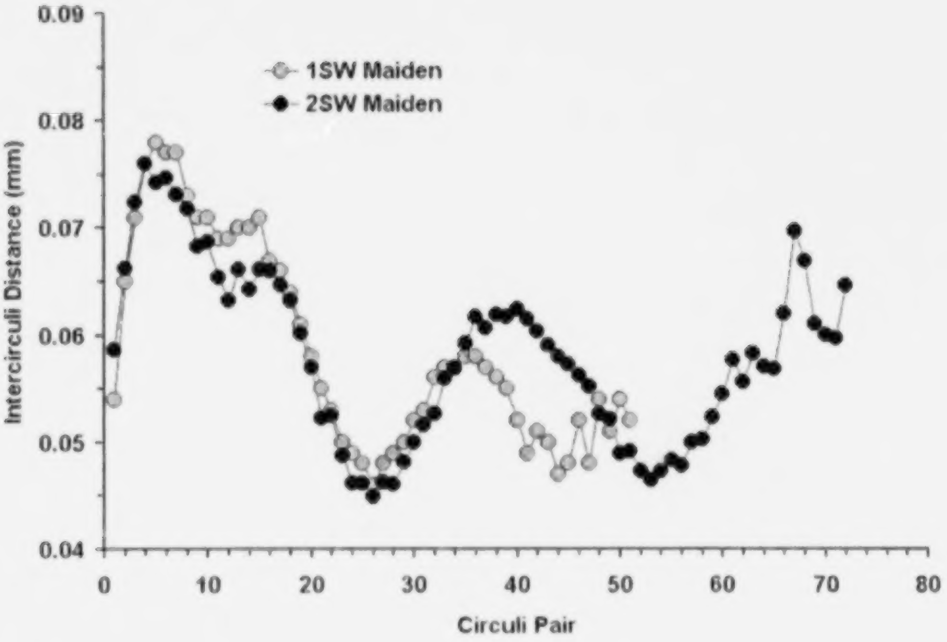


Figure 5. Average intercirculi spacing profiles from scales of Atlantic salmon returning to the Margaree River as 1SW maiden and 2SW maiden spawners for three smolt cohorts. Intercirculi spacings are measured from the last circulus of freshwater growth to the last circulus of marine growth at the edge of the scale.

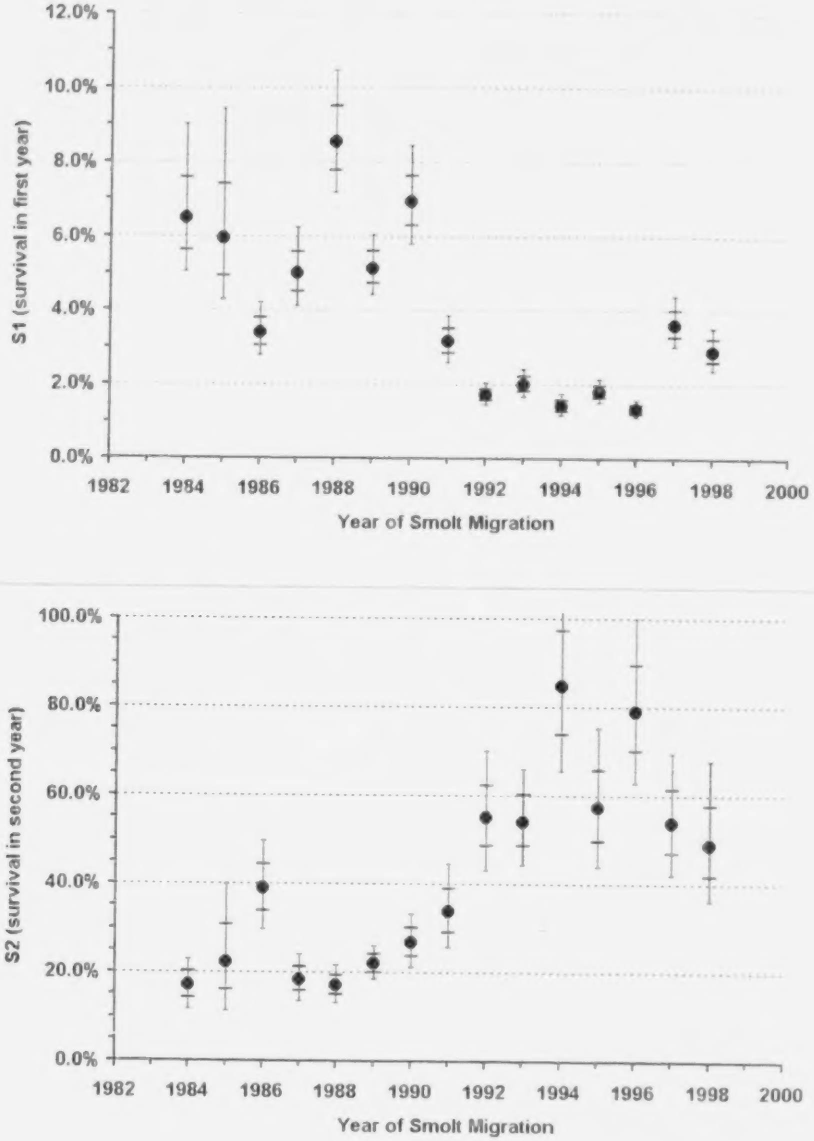


Figure 6. Solutions for S_1 (upper) and S_2 (lower) for Atlantic salmon from de la Trinité River. Bullets are the median value, dashes are the 25th and 75th percentiles, vertical lines define the 10th to 90th percentiles. A total of 5,000 simulations were performed.

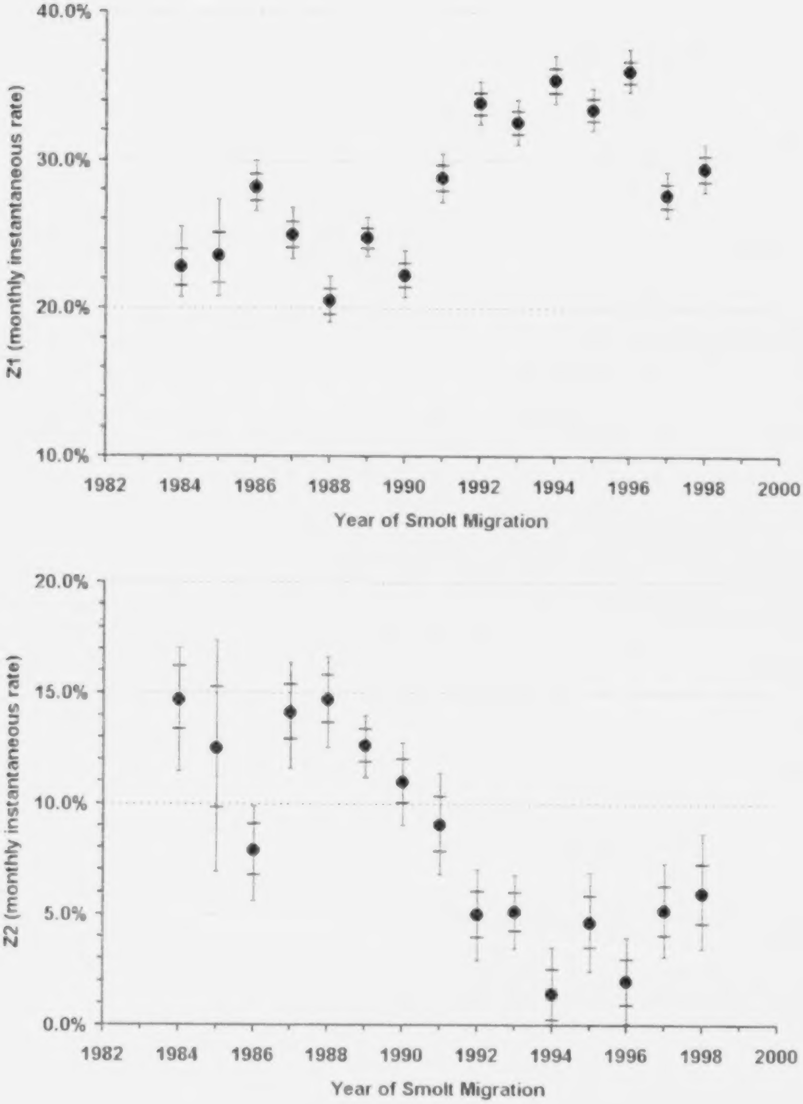
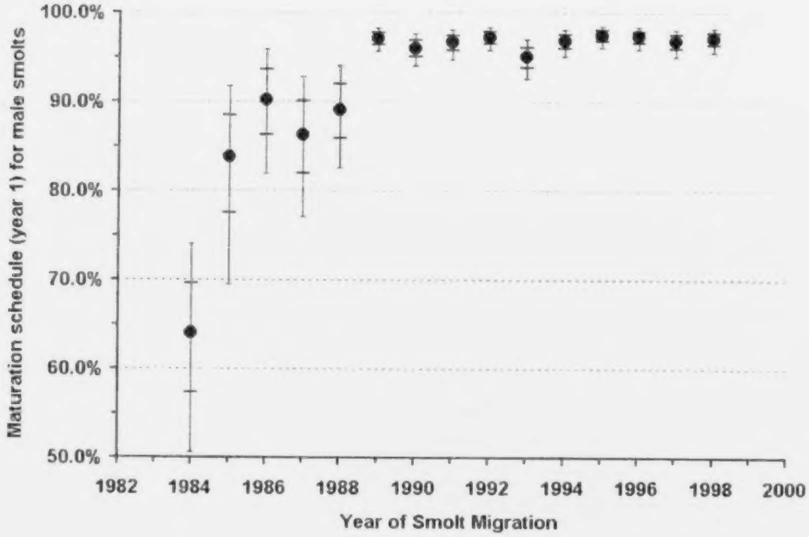


Figure 7. Solutions for the instantaneous monthly mortality rates Z_1 (upper) and Z_2 (lower) for Atlantic salmon from de la Trinité River. Bullets are the median value, dashes are the 25th and 75th percentiles, vertical lines define the 10th to 90th percentiles. A total of 5,000 simulations were performed.



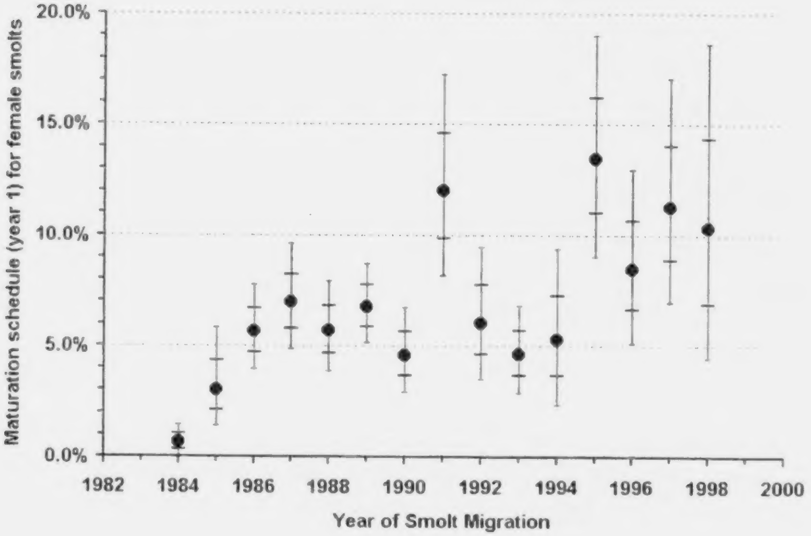


Figure 8. Solutions for the proportion of male (upper) and female (lower) smolts which mature at 1SW of age for de la Trinité River. Bullets are the median value, dashes are the 25th and 75th percentiles, vertical lines define the 10th to 90th percentiles. A total of 5,000 simulations were performed.

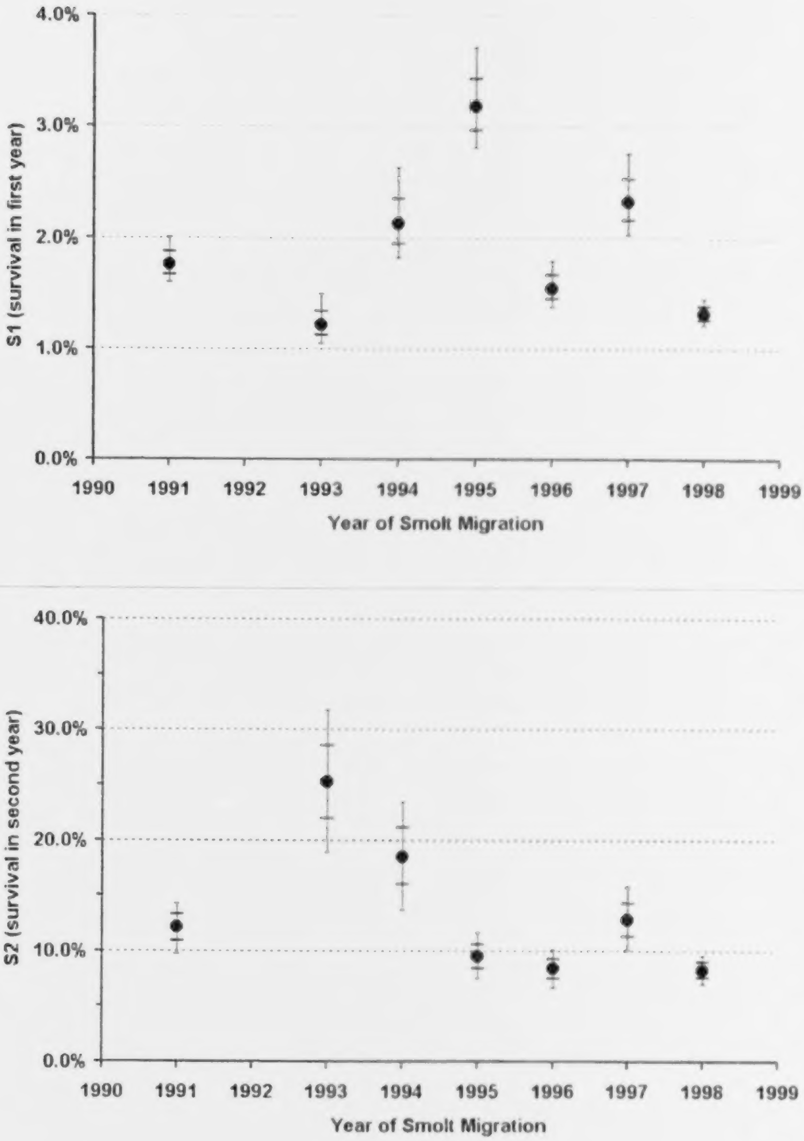


Figure 9. Solutions for S_1 (upper) and S_2 (lower) for hatchery return Atlantic salmon from Saint John River at Mactaquac. Bullets are the median value, dashes are the 25th and 75th percentiles, vertical lines define the 10th to 90th percentiles. A total of 5,000 simulations were performed.

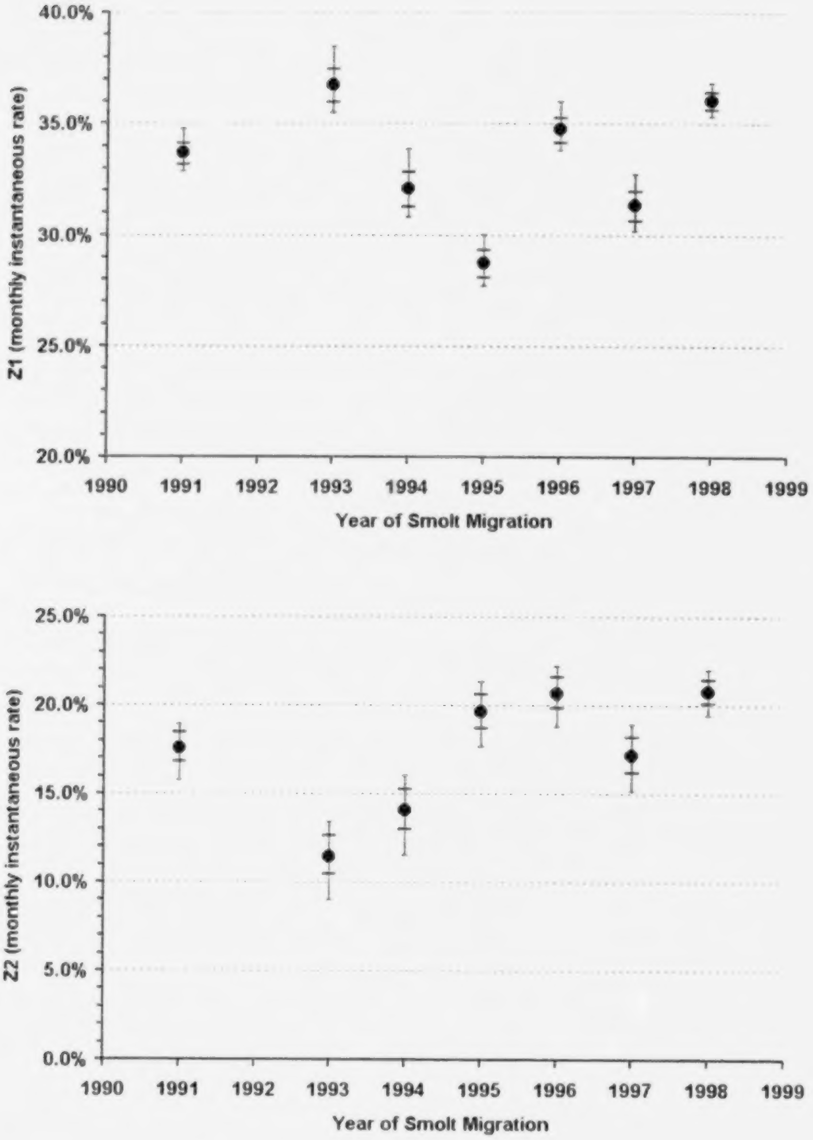


Figure 10. Solutions for the instantaneous monthly mortality rates Z_1 (upper) and Z_2 (lower) for hatchery origin Atlantic salmon from the Saint John River at Mactaquac. Bullets are the median value, dashes are the 25th and 75th percentiles, vertical lines define the 10th to 90th percentiles. A total of 5,000 simulations were performed.

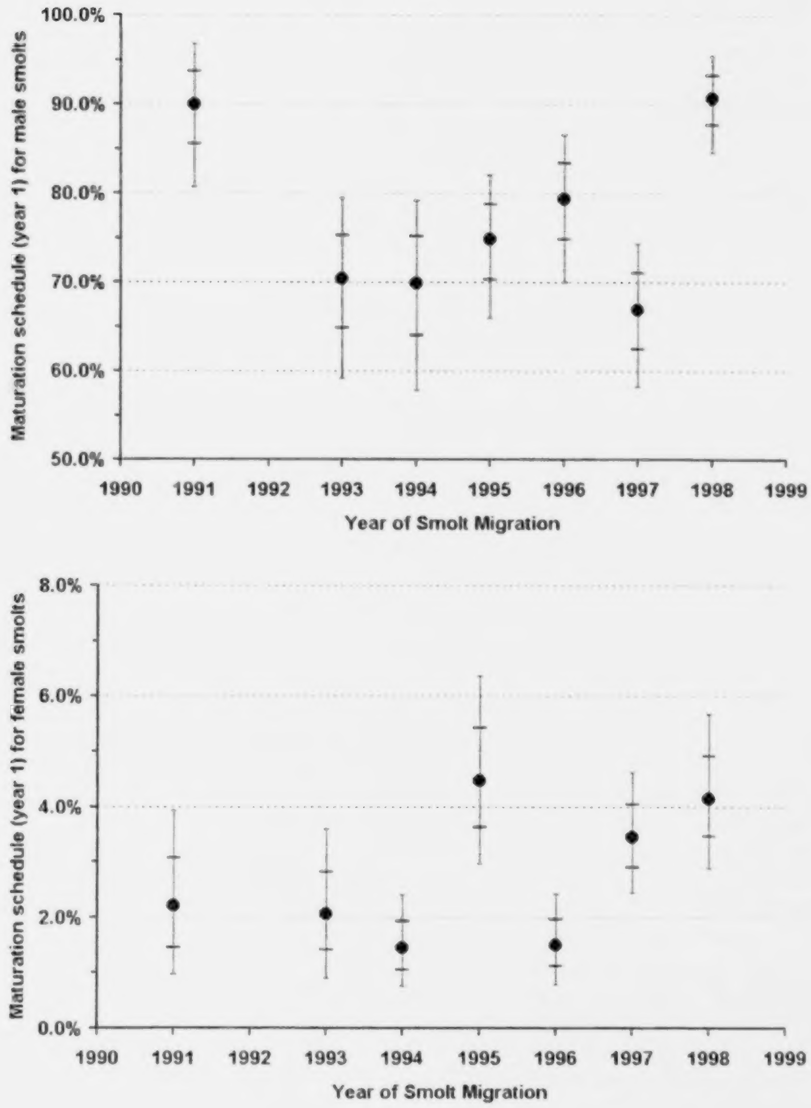


Figure 11. Solutions for the proportion of male (upper) and female (lower) hatchery one-year old smolts which mature at 1SW of age for Saint John River at Mactaquac. Bullets are the median value, dashes are the 25th and 75th percentiles, vertical lines define the 10th to 90th percentiles. A total of 5,000 simulations were performed.

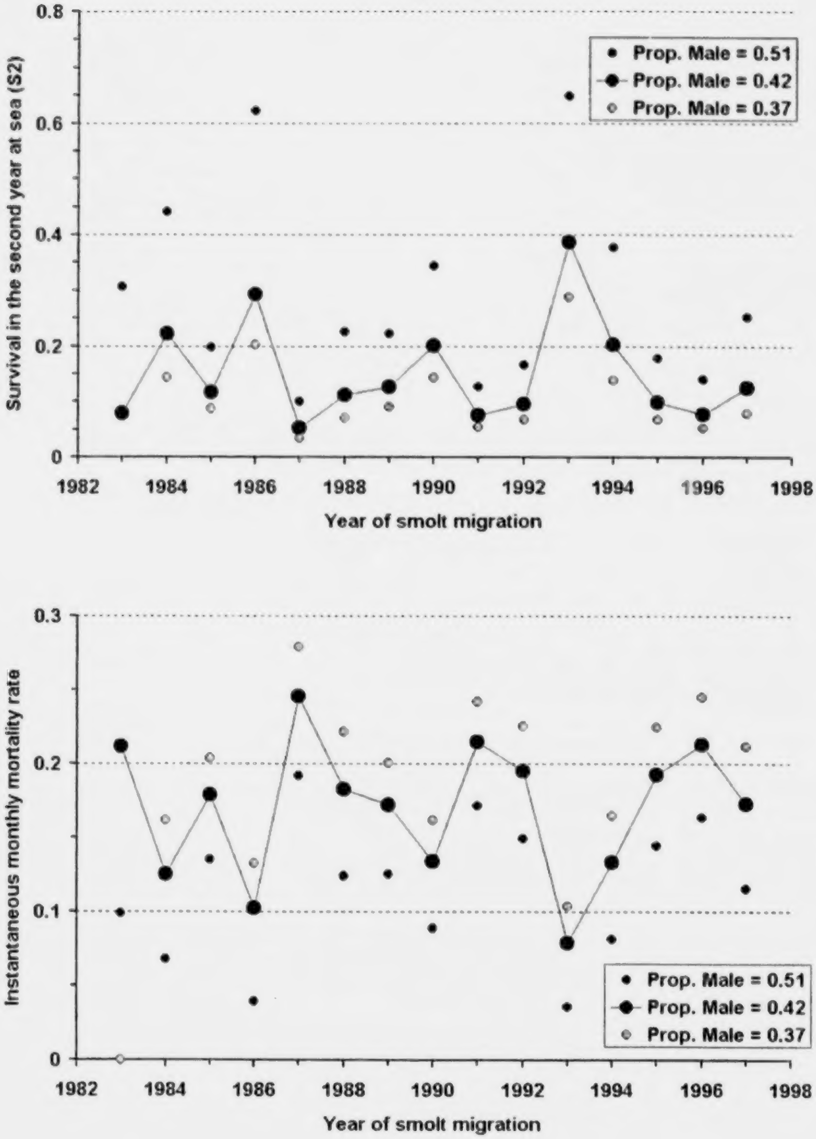


Figure 12. Solutions for S_2 (upper) and instantaneous monthly mortality rate (lower) for wild Atlantic salmon from the Miramichi River.

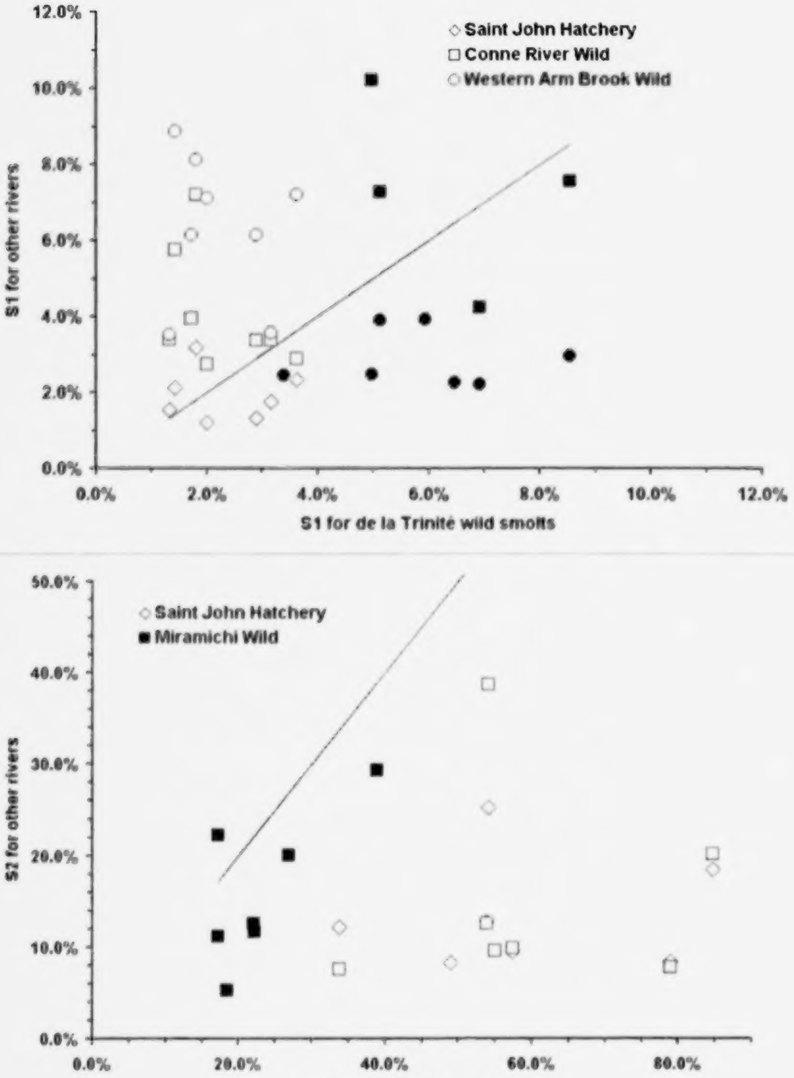


Figure 13. Comparative survival rates in the first year at sea (S1; upper) and in the second year at sea (S2; lower) of de la Trinité River wild smolts and other rivers in eastern Canada. The symbols in black represent the smolt runs prior to the commercial fishery moratorium in Newfoundland (1992). The diagonal line is the survival equivalency line.

6

MARINE NATURAL MORTALITY OF ATLANTIC SALMON (*Salmo salar* L.) IN ICELAND

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INTRODUCTION

In modeling the life cycle of Atlantic salmon (*Salmo salar* L.) it is essential to know the level of natural mortality (M) at each life stage. It is also important to measure or predict major factors that may affect natural mortality, such as changes in environmental factors. Such changes have been shown to explain some of the variation in the grilse to salmon ratio (Gudjonsson et al. 1995). However, estimates of M for fish are often difficult to obtain. For salmon there are numerous estimates of M for the freshwater stages since populations can be readily monitored in freshwater. Estimates of M during the marine phase are more difficult to obtain, particularly if the stock is exposed to both natural and fishing mortality factors at sea (Chaput 2003) or if there is a desire to estimate M at different stages in the marine phase.

The marine mortality for one sea-winter salmon (1SW) in the North Atlantic may be estimated from the proportion of tagged smolts returning as adult fish, if the majority of the stock returns as 1 SW salmon. Different levels of natural mortality for 1SW salmon have been observed in different parts of the North Atlantic and a significant downward trend has been observed for the return rates of monitored stocks as 1SW fish over the past 5- and 10-year periods (ICES 2000). This reduction in survival has not been fully explained. Some studies suggest that mortality is highest during the first few weeks after the smolt migration (Scarnecchia et al. 1989). Stocks of Atlantic salmon show different life history patterns and reproductive strategies. Determination of the scale, rate and direction of life history responses to environmental influence on growth rate and survival are essential for understanding the salmon life cycle (Hutchings and Jones 1998)

It has generally been assumed that natural mortality of Atlantic salmon after the first year at sea is likely to be low (Doubleday et. al 1979; Potter and Crozier 2000). Estimates of M for the second year at sea are more difficult to obtain than for the first sea year because of the possible interaction of factors affecting age at maturity. Although the life history pattern may be controlled by genetic factors, environmental factors can affect their expression (Futuyma 1979).

The absence of ocean fisheries for salmon in Icelandic waters simplifies studies of natural mortality on Icelandic stocks. Levels of natural mortality have therefore been estimated using Murphy's Method (Murphy 1952; Ricker 1975) on stocks where the sex ratios of smolts and returning adults are known. The results indicated that M for Icelandic salmon stocks could be high, 42-60% during the second year at sea (Tomasson et al. 1987; Jonasson et al. 1994). In this study, Murphy's method was used to calculate mortality during the second year at sea for hatchery-reared smolts released in the River Midfjardara, North Iceland. We also looked at the long-term trends in the grilse (1SW) to salmon (2SW) ratio as well as the sex ratio of salmon stocks in Iceland.

MATERIAL AND METHODS

In multi-sea-winter stocks of Atlantic salmon, males and females tend to proportionally mature at different ages. This feature provides an opportunity to estimate the survival during the first (S1) and second years (S_2) (Chaput et al. 2003). One method described by Ricker (1975, 1976) is called the Murphy method. Murphy (1952) realized the possibility of estimating mortality of salmon at sea based on multiple ages of at maturity of returning adults. Murphy's method assumes that the survival rates of male and female smolts at sea are the same and that the survivals of maturing and non-maturing fish during the first year at sea are the same. Murphy (1952) provided a solution for the survival in the second year at sea assuming that the sex ratio of smolts was 1:1. Ricker (1975) provides the derivation of the equations for ratios, which may differ from 1:1.

Defining the following:

F_1: Number of females returning as grilse (one-sea-winter salmon or 1SW)

F_2: Number of females returning as salmon (two-sea-winter salmon or 2SW)

M_1: Number of males returning as grilse

M_2: Number of males returning as salmon

m/f: sex ratio of smolts

then

$$S_2 = (m/f * F_2 - M_2) / (M_1 - m/f * F_1) \qquad (1)$$

If additionally, the total migration of male and female smolts is known, then estimates of S1 can also be obtained.

Let

M_0: Number of male smolts leaving the river

F_0: Number of female smolts leaving the river

then survival during the first year at sea (**S_1**) is:

$$S_1 = ((M_2+F_2) * 1/S_2+M_1+F_1) / (M_0+F_0) \qquad (2)$$

Mortality (A) is then calculated as the difference from the estimated survival rate:

$$A = 1 - S \qquad (3)$$

Murphy's method (Equation 1) was applied to a data set derived from simultaneous releases of 1 and 2 year old smolts into the River Midfjardara North Iceland for the years 1994-1997. Eggs were obtained from salmon caught in the river and juveniles were reared for 1 and 2 years. There were about 5,000 smolts in each group. The smolts were tagged with coded microwire tags so every individual smolt could be identified later. The adipose fin of all tagged smolts was cut off to enable identification of tagged fish. The smolts were initially released in a pond fed by river water and after 24 hours of acclimation in the pond the outflow was opened. The smolts were fed in the pond and generally stayed there from several days to a few weeks depending on the river water temperature before migrating to sea. Both 1 and 2 year old smolts were released in the same pond, except in the first year, when only 1 year olds were released. The sex ratio of each group of smolts was estimated from a random sample of 200 individuals.

Every salmon caught in the rod fishery in River Midfjardara was examined to sample tags and their sex and size recorded by trained individuals in the fishing hut at the river. Salmon from each group of smolts returned 1 and 2 years after they were released. The returns in the catch were used in the calculations in the present study. The exploitation rate during the study period was not available so total returns could not be calculated although this would have been preferable.

During the years 1988 to 1995 the exploitation rate of salmon in the River Midfjardara was calculated in relation to the salmon run in the river (Gudjonsson et al. 1996). The exploitation rate did not change significantly with variable size of the run of salmon. Therefore, this should not affect greatly the comparison of the result between years in present study. However, the average exploitation of 2SW salmon (0.85) was higher than that for 1SW salmon (0.70). This will have affected the calculation of S in present study and the comparison of survival of 1SW and 2SW salmon.

We also investigated how the grilse to salmon ratios in the River Laxa and the River Vididalsa, North Iceland varied over the period 1974 to 2000. The level of natural mortality in the River Laxa during the second year at sea was calculated using the Murphy method. The sex ratio of smolts was unknown but we assumed that there were equal numbers of males and females in the outgoing smolts.

As for most Icelandic rivers accurate rod catch statistics are available for the Laxa and Vididalsa, and fishing effort has remained stable because a fixed number of rods and angling days are allowed. We therefore assumed that the exploitation rates were constant over time and therefore the rod catches were directly equivalent to relative abundance or stock size (Gudjonsson et al. 1995). The rod catch statistics as recorded in logbooks, it provides information on the number of salmon, sex, sea age, weight and date of every salmon caught. The ratio of males and females were obtained from the logbooks for both the 1SW and 2SW components of the catch.

RESULTS

There were equal numbers of males and females in all the smolt groups released in River Midfjardara, and the ratio did not differ significantly from 1:1. Therefore am/f ratio of 1 was used.

The return rate and mortality at the second year at sea for the different smolt groups in Midfjardara varied. In most cases the return rate was lower for one-year-old smolts (Table 1).

There was no significant correlation between the total return rate of fish and survival during the second year at sea.

The catch of 2SW salmon in the River Laxa was higher than the catch of 1SW salmon in the earlier part of the study period with a change in the mid 80s (Fig. 1). No trend was seen in number of 1SW salmon during the same period. A similar pattern can be seen for catches in the River Vididalsa for the same period (Fig. 2).

The calculated mortality of salmon during the second year at sea in the River Laxa showed large variations with an increasing trend in mortality in later years (Fig. 3). However, the mortality rate estimates were frequently negative especially in the earlier period (before 1985). Negative values for A are nonsense values which indicate that some of the assumptions of the Murphy method or of the input data were invalid including sex ratios of smolts which differed from 1:1 over the time series, exploitation rates on 1SW and 2SW which changed over time, mortality rates on smolts differing between maturing and non-maturing fish in their first year and between males and females.

The sex ratio of both 1SW and 2SW fish in the annual catches varied during the study period but no trend can be seen in the data for the salmon catch in the River Laxa (Fig. 4) or the River Vididalsa (Fig. 5).

DISCUSSION

The limited results from the River Midfjardara support the hypothesis that mortality of Atlantic salmon during the second year at sea is high and variable.

The return rate was generally low for the smolt releases in the River Midfjardara, and the majority of the fish returned as 1SW salmon. However returns of 2SW salmon occurred in most groups with the exception of the group of 2 year old smolts in 1996. Survival during the second year at sea was generally low, but survival during the first yer was even lower. Variations in mortality from year to year can also be seen. Since the largest part of the mortality at sea occurs during the first year and is variable, it is not surprising that there is no correlation between the return rate and mortality during the second year at sea.

The marine mortality in the second year at sea for the River Midfjardara salmon is higher than found in research for hatchery stocks in West Iceland in 1988-1990 (Jonassson et al. 1994). This may indicate that marine mortality in the second year at sea has been higher in recent years and/or is higher in the north.

The negative mortality rate values for the River Laxa are indicative of the limits of our assumptions although for this data set, we do not know which assumption(s) was violated.

There has been a downward trend in the number of salmon (2SW) in most rivers of Iceland in recent decades (Gudjonsson et al. 1995), and the trends for 2SW salmon in Laxa and Vididalsa are no different. The proportion of 2SW salmon in catches for both rivers has been lower since 1984 than in earlier years. This change occurred quite suddenly suggesting that it was not the result of genetic changes. At a similar point in time this trend has been observed in general for rivers around the North Atlantic (ICES 2000). The present study perhaps indicates that the mortality is variable between years as has been seen in other studies (Gudjonsson et al. 1995). Furthermore it shows the same trend, i.e. mortality during the second year at sea has increased in the latter part of the study period. The fishing effort in Laxa and Vididalsa remained unchanged during this period so it is unlikely that changes in fishing mortality rates in the river can explain these estimated changes in mortality.

A possible explanation for the decreased catches / abundance of 2SW salmon is that more fish are returning as grilse perhaps due to different growth rates in freshwater (Chadwick et al. 1987) or at sea (Friedland and Haas 1996). If that was the case, we would have expected to see a change in the sex ratio of the adults, either more females in the 1SW stage or fewer males in the 2SW stage.

The sex ratios of the 1SW and MSW salmon in the Laxa have varied from year to year but have shown no trends. This suggest that the genetic expression of sea age at maturity has not changed, at least during this study period in the rivers Laxa and Vididalsa, however decreased survival during the salmon's second year at sea has led to fewer fish returning as 2SW adults. The mechanisms for this are not clear as for so many aspects of the salmon life cycle at sea.

It seems likely that salmon migrate to different areas during their first and second years in the sea because there is no correlation between the survival rates for the two groups. Possible explanations for increased mortality are higher predation and reduced food availability in the feeding areas for 2SW salmon. It is also possible but less likely that the two size groups of salmon are affected differently in the same area. Another and more speculative cause could be that fish that spend longer at sea may be more susceptible to factors related to human activities such as chemical contaminants having direct or indirect effects through the food chain as suggested by Scott (2001). Some of these questions could be studied if a greater number of data sets with sex ratio and abundance estimates of smolts and returning adults were available.

ACKNOWLEDGEMENTS

We would like to thank Ted Potter and Gerald Chaput for valuable suggestions and comments for improving the manuscript.

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Table 1. Return rate(%) and mortality at sea of different smolt groups in Midfjardara

			Second year at sea		First year at sea	
Year of release	Smolt age	Total return %	Survival (%)	Mortality (%)	Survival (%)	Mortality (%)
1994	1	1.53	28.48	71.52	2.19	97.81
1995	1	0.91	-	-	-	-
1995	2	0.92	25.75	74.25	1.21	98.79
1996	1	0.0	-	-	-	-
1996	2	0.14	-	-	-	-
1997	1	1.45	12.77	87.23	2.27	97.73
1997	2	2.76	4.60	95.40	4.48	95.52

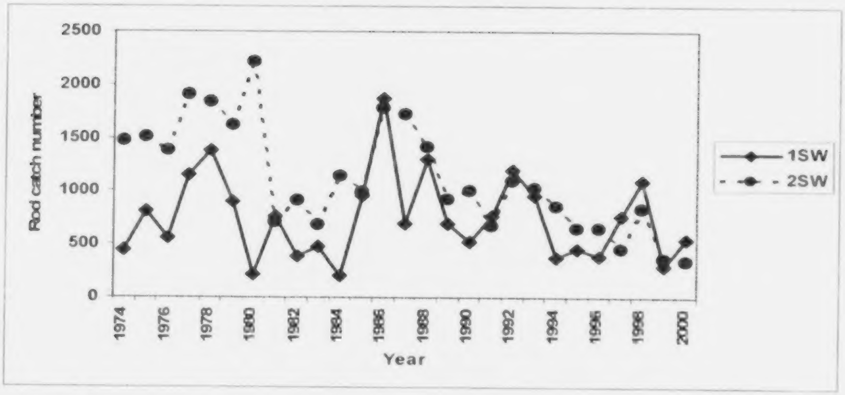

Figure 1. The number of 1SW and 2SW salmon caught in the River Laxa 1974-2000.

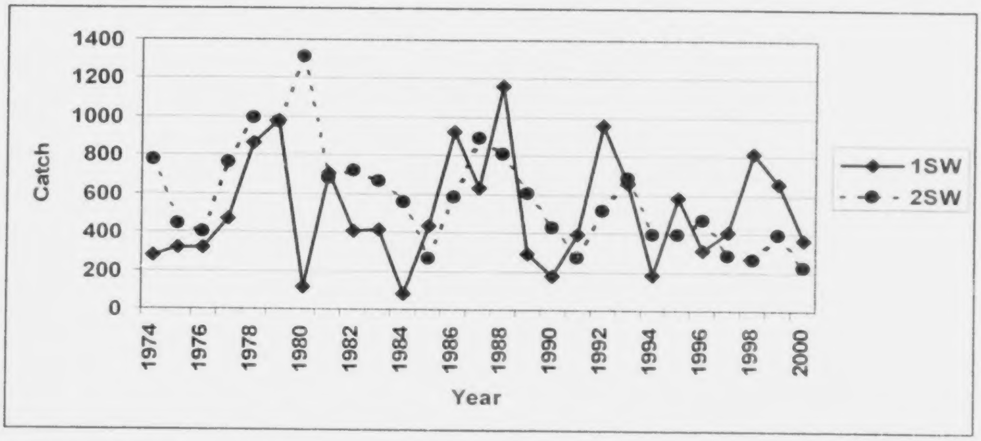

Figure 2. The number of 1SW and 2SW salmon caught in the River Vididalsa 1974-2000

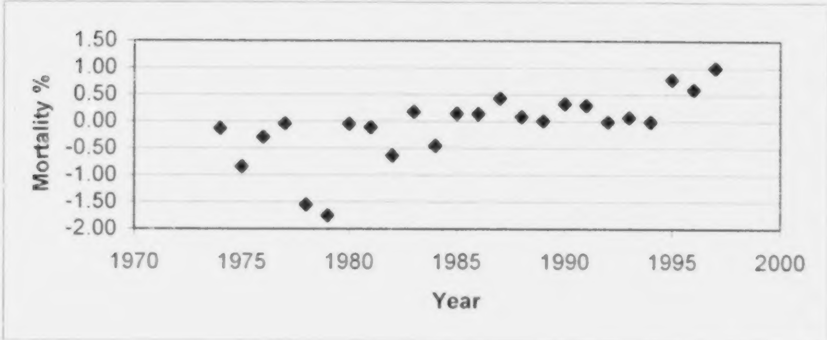

Figure 3. Calculated mortality (A expressed as %) during the second year at sea in the River Laxa assuming equal number of males and females in the smolt run.

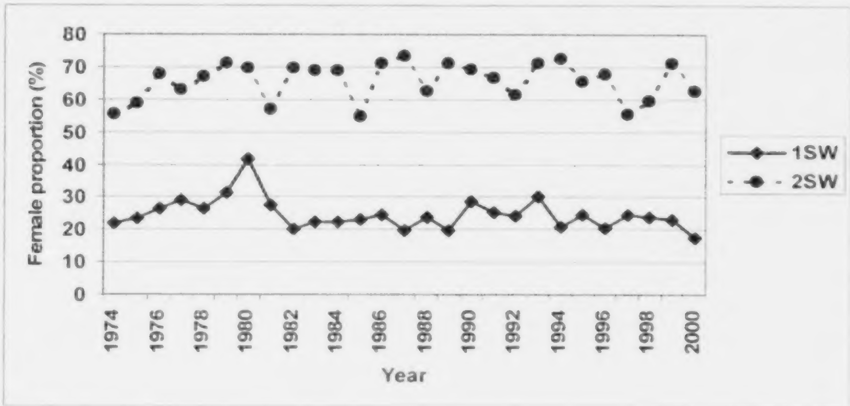

Figure 4. Percent female in the 1SW and the 2SW salmon catches in the River Laxa 1974-2000.

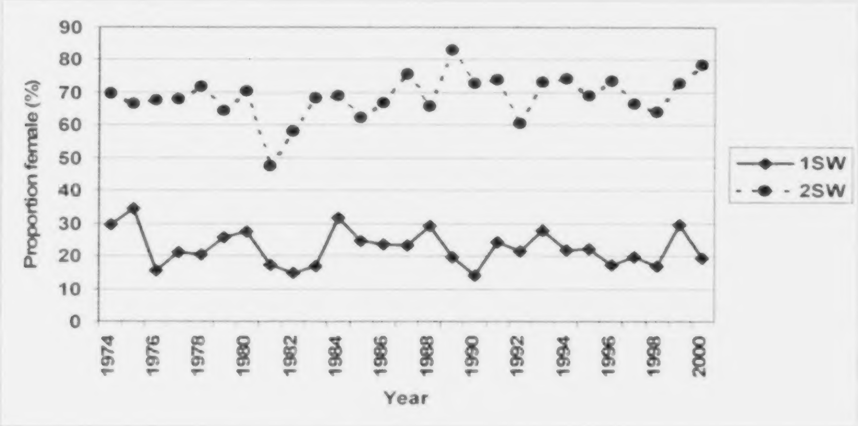

Figure 5. Percent female in the 1SW and 2SW salmon catches in the River Vididalsa 1974-2000.

7

CHANGE IN SIZE SELECTIVE MORTALITY IN ATLANTIC SALMON (*Salmo salar* L.), DE LA TRINITÉ RIVER, QUÉBEC, CANADA

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INTRODUCTION

The total population of 1SW and 2SW Atlantic salmon (*Salmo salar* L.) in the northwest Atlantic has oscillated around a generally declining trend since the 1970s (ICES 2001). Abnormally high marine mortality, seemingly common to all North American Atlantic salmon populations, has been observed in recent years (O'Neil et al. 2000). On de la Trinité River, marine survival has fluctuated from a high of 4.53% in 1988 to a low of 0.69% in 1999. The mean annual smolt survival rate was 2.21% for the period 1984-1999; for the period 1984-1991, average sea survival ws considered to be normal at 2.96% compared with 1.40% for the period 1992-1999, a period we qualify as a low-survival period (Fig. 1).

One way to address the question of mortality patterns at sea is to use biological material already collected and measured to see if size selective mortality has changed in recent years compared to years characterised by better survival at sea.

The goal of this paper is to present preliminary data on changes in size selectivity mortality observed in the last decade.

METHODS

Study areas

Located on St-Lawrence North-Shore in zone Q7, de la Trinité River is 60 km long and its drainage area of 562 km^2 is entirely forested. Total fluvial habitat accessible for salmon is 2.11 million m^2 and juvenile salmon habitat has been estimated at 0.99 million m^2 (Caron et al. 1999). A conservation limit has been set at 1.63 million eggs.

Population characteristics

Annual smolt estimates are available since 1984. During the migration, 1 to 6 smolt sub-samples are taken on a daily basis to permit measurement of total length, fork length (FL) and weight, to determine sex, and to collect scales samples for ageing and measurement.

Adults returning to the river must pass through a fish ladder that permits a count of all salmon and their classification as 1SW or MSW salmon based on total length (i.e. salmon les than or equal to 65 cm in fork length are considered as 1SW and the larger salmon are classified as MSW). A recreational fishery is permitted in this river and registration of each salmon is compulsory. The biological characteristics of these fish are recorded and scales samples are taken for growth analysis.

Smolt year classes are always dominated by 3 yr-old fish which represent on average 77% of the run; 13% of the run are 2 yrs and 10%, 4 yrs. Annual mean size (FL) of 3 year old smolts is 121 mm (min 112, max 132). It has changed from an average of 119 mm for the period 1984 to 1991 to 124 mm for the period 1992-1999 (Table 1).

In the past, marine survival of de la Trinité River salmon has fluctuated from the highest rate of 4.53% in 1988 to the lowest rate of 0.69% in 1999 and shows a mean survival rate of 2.21%. Survival at sea of the 1999 cohort is the lowest encountered over the past 16 years (Fig. 1).

In order to compare patterns in size-selective mortality between periods of normal and low sea survival, 3-yr-old smolt from 1984 and 1985 (normal sea survival) and from 1994 and 1995 (low sea survival) and the adults returning from these cohorts after 1 and 2 years at sea were analysed to compare size at smoltification during outmigration with size at smoltification of survivors as back-calculated from the scales of returning adults.

Scale measurements

Scales were mounted on glass slides. For the smolts, total radius (RT) of the scale was measured on the vertical and central axis. For the adults, total radius (RT), radius at smoltification (RS) and radius at the end of the first year of growth in sea (R1) were measured. The standard lengths of salmon at smoltification were back-calculated from returning adults using the biological intercept technique (Campana and Jones 1992)

Statistical analysis

One-factor analysis of variance was conducted for each smolt cohort to compare smolt size at outmigration with the smolt size back-calculated from adult scales. A two-factor analysis of variance was conducted to compare changes in smolt sizes due to size-selective mortality between the two periods of normal (84-85) and low (94-95) sea survival.

PRELIMINARY RESULTS

Smolt lengths for each cohort were compared to the corresponding lengths at smoltification back-calculated from adults returning after one (1SW) and two years (2SW) at sea. In all cases, the mean smolt length back-calculated from the adult scales was greater than the mean lengths of the emigrating smolts, suggesting that there was selection against smaller smolts (Table 2).

The second analysis was conducted to determine if the selective mortalities on smaller smolt were different between years of better (84-85) or poorer (94-95) sea survival. The analyses showed significant increases in size selective mortality for the 1SW fish ($P<0.003$) and the 2SW fish ($P<0.001$) between periods, particularly for 2SW salmon (Fig. 2).

These preliminary results confirm the higher marine mortality of smaller smolts in recent years. Considering the fact that the commercial fishery was operating during the normal sea survival period and was closed during the poor survival period, this suggests that natural mortality (M) had increased in recent years. This may be explained by an increased in predation or a change in environmental conditions such as water temperature. However, other studies are needed to test these hypotheses.

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Table 1. Smolt characteristics from de la Trinité River, 1984-2001.

Year	Abundance	N	Mean Age	Condition Factor	Percent at age				% Female	Mean Fork Length (mm)
					2	3	4	5		
1984	68 208	284	2.88		14	85	1	0	63	
1985	66 069	86	2.90		17	76	7	0	53	131
1986	96 545	207	3.01		8	82	10	0	59	124
1987	77 617	221	3.10		5	79	16	0	55	129
1988	51 879	228	2.73	0.97	37	54	10	0	56	131
1989	80 057	313	2.79	0.97	28	66	6	0	56	132
1990	50 328	193	3.07	0.83	8	78	13	1	63	127
1991	40 863	163	3.08	0.92	8	76	16	0	61	132
1992	50 869	205	3.03	0.92	9	78	13	0	55	136
1993	86 226	265	3.03	0.94	6	85	8	1	68	138
1994	55 913	144	3.03	0.96	9	79	11	1	58	132
1995	71 899	220	3.01	0.95	15	69	16	0	55	134
1996	61 092	193	3.05	0.95	4	88	9	0	55	130
1997	31 892	213	3.09	0.94	7	77	16	0	60	133
1998	28 962	171	3.08	0.97	10	72	18	0	57	143
1999	56 557	137	2.87	0.94	21	71	8	0	59	131
2000	39 744	110	2.88	0.94	23	66	11	0	56	133
2001	70 318	150	2.93	0.96	11	86	3	0	57	134
Mean	60 280		2.97	0.94	14	76	10	0	58	132

Table 2. Analysis of variance of observed mean smolt size and mean length-at-smolt back-calculated from adult returns of the same cohort after one and two years at sea. *P < 0.005 in all cases.

Smolt cohort		Observed Smolt	Back-calculated 1SW	2SW
1984	Mean length (cm)	13.1	14.2	14.2
	F-ratio		**29.5***	**27.5**
1985	Mean length (cm)	12.0	14.1	14.1
	F-ratio		**55.6***	**86.2***
1994	Mean length (cm)	12.3	14.1	16.0
	F-ratio		**46.2***	**171.5***
1995	Mean length (cm)	12.4	15.2	15.6
	F-ratio		**139.4***	**134.1***

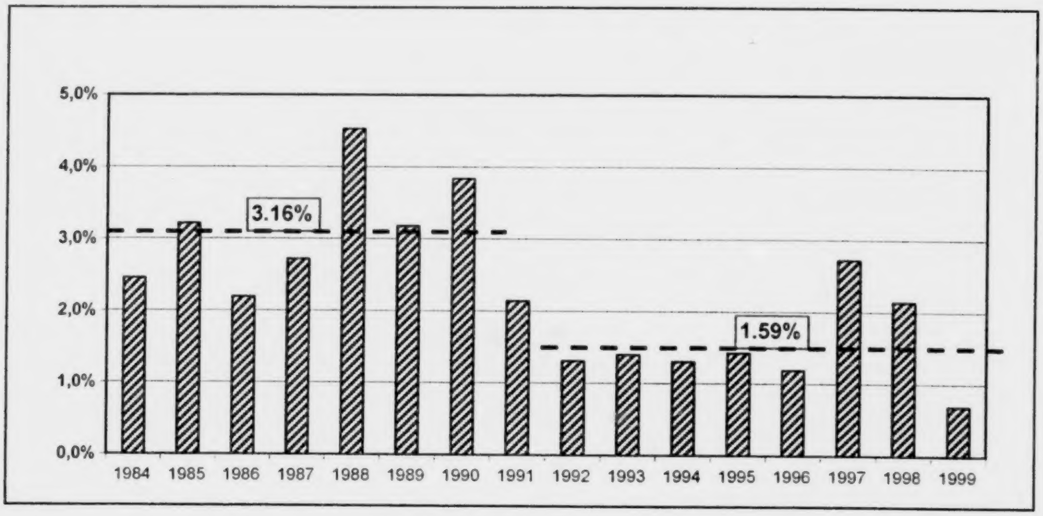

Figure 1: Sea survival of smolts from de la Trinité River. Year refers to the year of smolt migration.

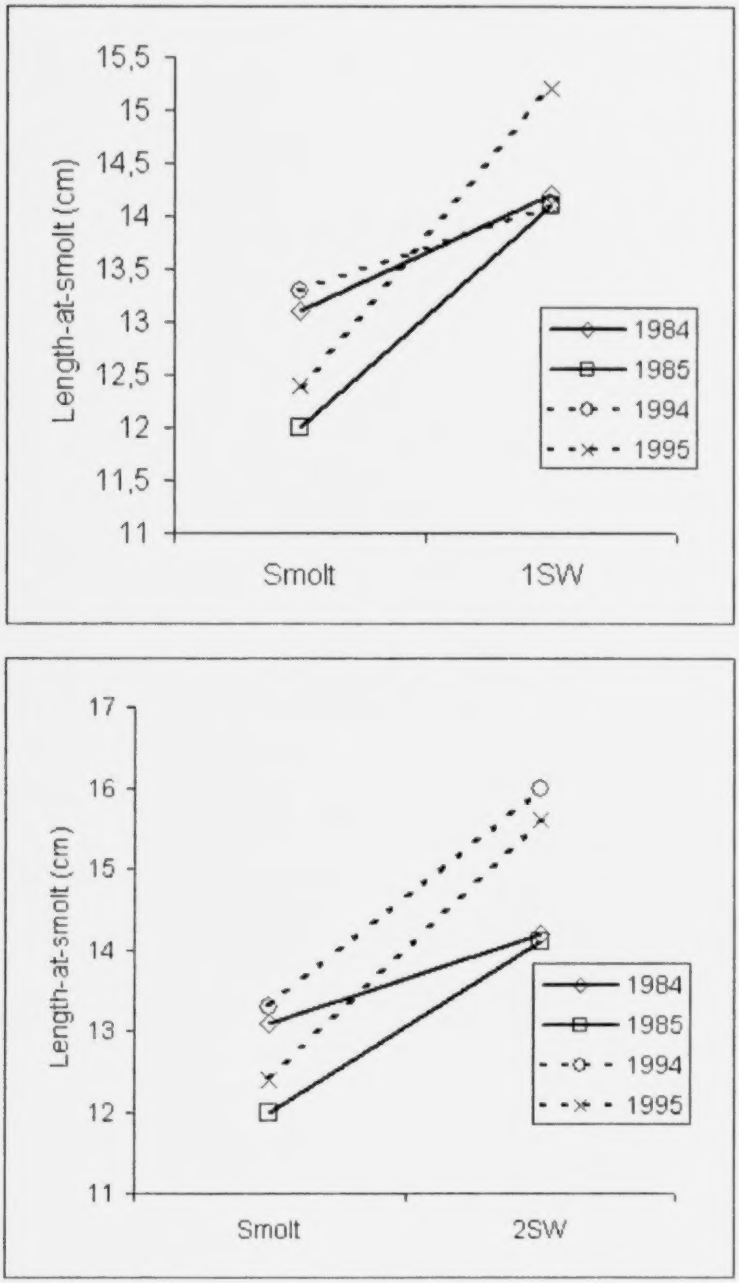

Figure 2: Back-calculated length at smolt stage of 1SW and 2SW salmon compared to the observed length of smolts for the different years. Back-calclated lengths for 1994-1995 period were significantly longer than for the 1984-1985 period for 1SW ($F = 9.07$; $P < 0.003$) and 2SW salmon ($F = 57.3$; $P < 0.001$).

8

FRESHWATER INFLUENCES ON MARINE SURVIVAL OF ATLANTIC SALMON (*Salmo salar* L.): EVIDENCE FROM THE RIVER BUSH, NORTHERN IRELAND.

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INTRODUCTION

The River Bush is 67 km long and has a total catchment area of around 340 km². It rises in northeast Ireland, and enters the Atlantic Ocean on the Co. Antrim coast. The river has no estuary, entering the sea across a stony beach. During the early 1970s the Department of Agriculture for Northern Ireland[1] set up traps at Bushmills, 3 km from the river mouth, to count descending smolts and ascending adults, in order to study the population dynamics of the wild Atlantic salmon (*Salmo salar* L.) population (Crozier and Kennedy 1991). The Department controls angling on the river, with day tickets requiring catch returns to be made. Data on rod catches downstream of the traps are thus available, to facilitate the total count of adult returns to freshwater. A hatchery strain, founded from the wild stock, is maintained at Bushmills for research into marine survival, exploitation, and other studies.

Data on marine survival of wild 1SW Atlantic salmon from the R. Bush are available from releases of coded wire tagged wild smolts. Returns of tagged fish to the river (trap and rods) and from tag recovery programmes in homewater fisheries around the Irish coast enable survival from smolt release to coastal return to be estimated using run-reconstruction techniques (Potter and Dunkley 1993). In the absence of significant exploitation of 1SW salmon in fisheries outside Irish coastal waters and following correction for tagging/handling mortality (Crozier and Kennedy 1994, 2003), these return rates represent estimates of true marine survival.

RESULTS AND DISCUSSION

Return rates of tagged 1SWwild salmon to Irish coastal waters were high and relatively stable in the earlier part of the time series, varying from 25% to 36% over an 11 year period during the 1980's to mid 1990's (Fig. 1), and averaging around 28%. However, survival rates have recently fallen sharply, with survival rates declining from 19.8% for the 1997 smolt year class to an all time low of 10.1% for the 2000 smolt year class.

A possible factor implicated in this decline may be related to the timing of the wild smolt migration in this stock, which has not remained constant during this period. Examination of an index of wild smolt migration timing (date of the first smolt captured at the smolt trap), indicates that for the four recent years of particularly low marine survival the smolt run started around two weeks earlier than the previous average start date (Fig. 2). A significant relationship between marine survival and smolt migration date (Fig. 3, $r^2=0.72$, $P<0.01$) suggests that cohorts where the smolt run commenced earlier display poorer marine survival. Examination of the median date of smolt capture as an alternative measure of smolt run timing (Fig. 4), suggested a similar trend, though this was not as strong (Fig. 5, $r^2=0.31$ $P>0.1$). Because the smolt run timing is not normally distributed or uniform (starting and stopping according to flow and temperature fluctuations) the date of first smolt may give a better overall indication of the potential progression of the entire run than percentile dates. This is currently being examined. The date of the first smolt migration in 2001 returned to just within the previous "normal" range (Fig. 1) and will thus provide a test of this hypothesis, which would predict that marine survival would return to values close to the previous range.

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[1] *Now Department of Agriculture and Rural Development (DARD)*

A possible causal link between timing of smolt migration and subsequent survival at sea can be hypothesised, if early running smolts are migrating outside an "optimum" window for smolt entry to the sea (Hansen 1990). Certainly, smolt release data for hatchery reared R. Bush smolts released sequentially over a wide range of dates indicate that time of release has a significant effect on marine survival (Moffett et al. 2002; Kennedy and Crozier 2002), while Dempson et al. (2003) noted influences of varied wild smolt run timing on marine survival for several rivers in Newfoundland, Canada.

Alternative hypotheses to the influence of smolt migration timing were also tested for this stock, including biological characteristics of migrating smolts (size, condition factor and age composition of the smolt run).

Smolt age composition on the R. Bush is not stable, with large inter-annual variation in the relative proportions of 1+ and 2+ smolts (Fig. 6), which constitute the majority of the smolt run. As marine survival is not calculated separately by smolt age for this stock, it was not possible to directly test relationships between age at migration and marine survival. However, there were no overall temporal trends in smolt age composition for this stock, while relationships between the proportion of 1+ and 2+ smolts in the run and overall cohort survival were non-significant (Table 1). No trends in length, weight, or condition factor were apparent during the period tested and no significant relationships between these characteristics and marine survival were detected (Table 1).

Therefore, it may be the case that wild smolts from this river have recently been migrating outside the optimum window for survival, perhaps as a result of milder winter/spring conditions. Environmental data for the R. Bush catchment are currently being examined to try to further relate environmental conditions to smolt migration timing and to determine if migration timing can be predicted from environmental data.

If recent abnormally early smolt runs on the R. Bush are being driven by climate change, then these impacts may be expected on a wider group of rivers, which, if persistent, may have significant impacts on future salmon stock status.

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Table 1.Temporal trends in River Bush wild smolt biological characteristics and relationships with marine survival expressed as 1SW return to Irish coastal waters, 1986-2000.

Characteristic	Temporal trend	Marine survival
1+ smolt proportion	$r^2=0.125$, $P>0.1$	$r^2=0.008$, $P>0.1$
2+ smolt proportion	$r^2=0.126$, $P>0.1$	$r^2=0.010$, $P>0.1$
1+ smolt length	$r^2=0.003$, $P>0.1$	$r^2=0.028$, $P>0.1$
2+ smolt length	$r^2=0.223$, $P>0.1$	$r^2=0.034$, $P>0.1$
1+ smolt weight	$r^2=0.003$, $P>0.1$	$r^2=0.011$, $P>0.1$
2+ smolt weight	$r^2=0.342$, $P>0.1$	$r^2=0.146$, $P>0.1$
1+ smolt condition factor	$r^2=0.001$, $P>0.1$	$r^2=0.106$, $P>0.1$
2+ smolt condition factor	$r^2=0.025$, $P>0.1$	$r^2=0.126$, $P>0.1$

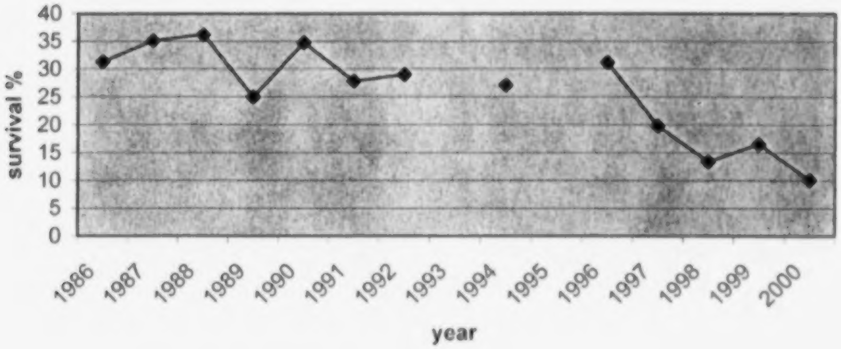


Figure 1. Marine survival (%) of wild 1SW River Bush salmon to Irish homewaters relative to year of migration.

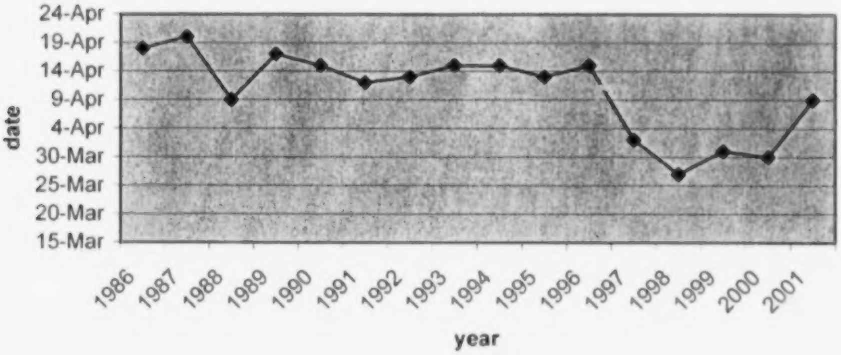


Figure 2. Date of first migration of River Bush smolts versus year.

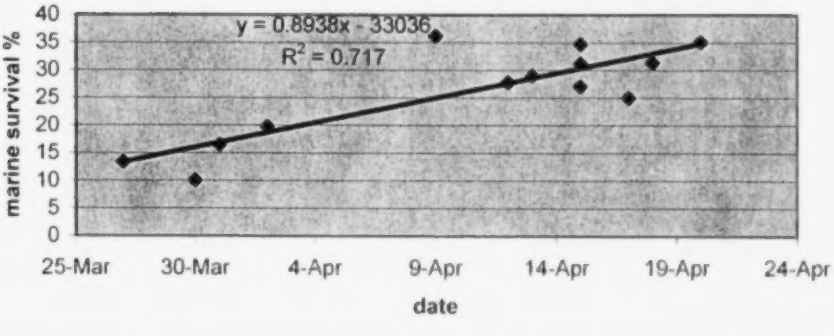


Figure 3. River Bush 1SW marine survival (%) to Irish homewaters relative to date of migration of first smolt.

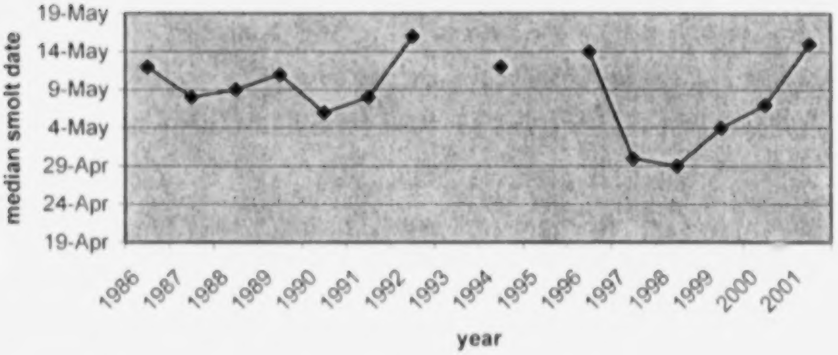


Figure 4. Median date of migration relative to year for River Bush smolts.

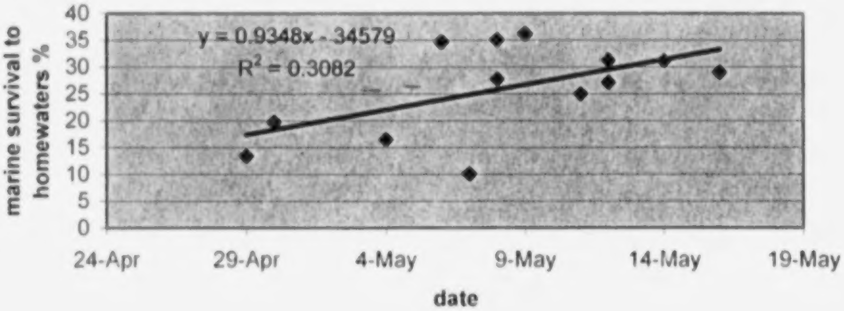


Figure 5. Marine survival (%) of River Bush 1SW salmon expressed as returns to Irish homewaters relative to median date of smolt migration.

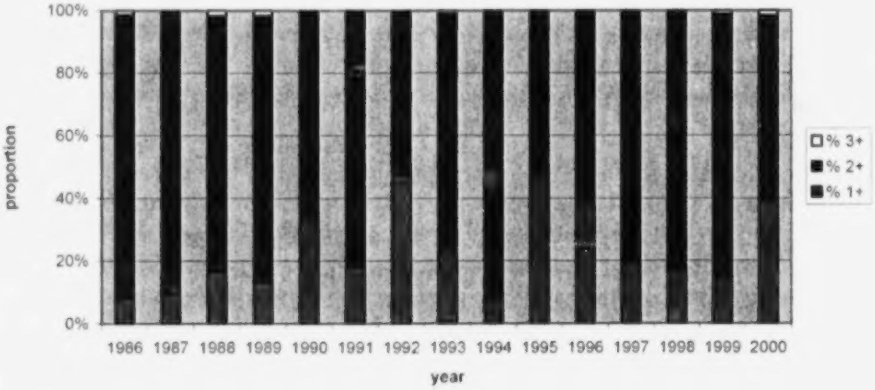


Figure 6. Proportions at age in the annual smolt run of River Bush Atlantic salmon.

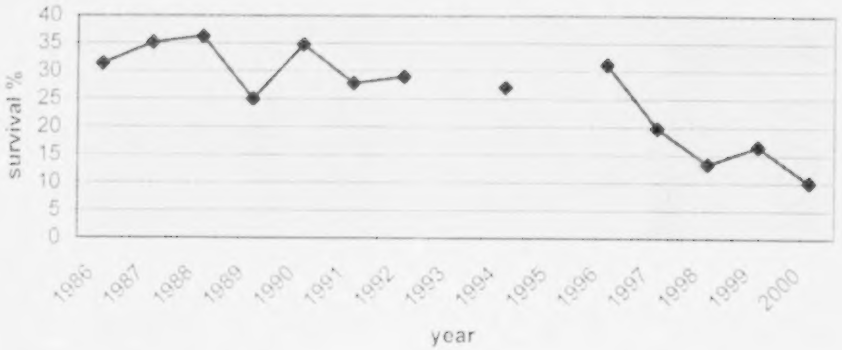


Figure 1. Marine survival (%) of wild 1SW River Bush salmon to Irish homewaters relative to year of migration.

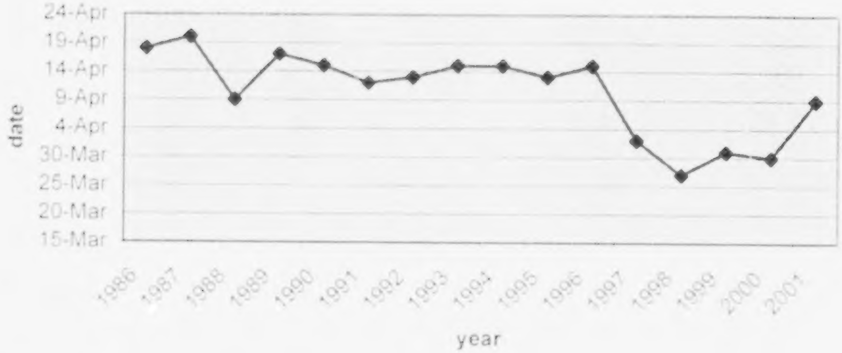


Figure 2. Date of first migration of River Bush smolts versus year.

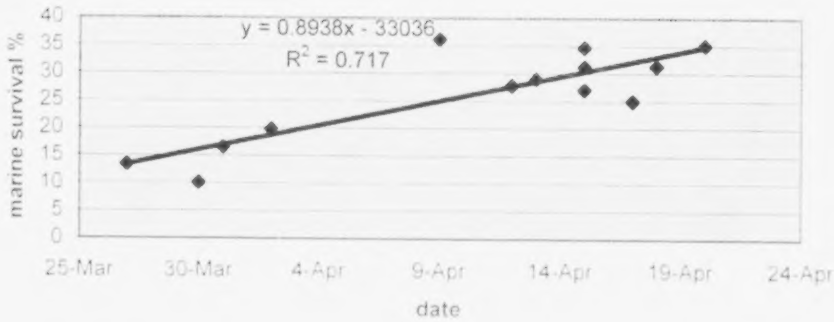
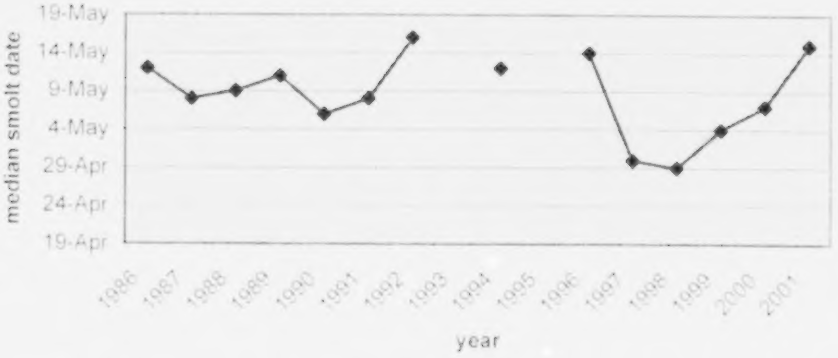


Figure 3. River Bush 1SW marine survival (%) to Irish homewaters relative to date of migration of first smolt.



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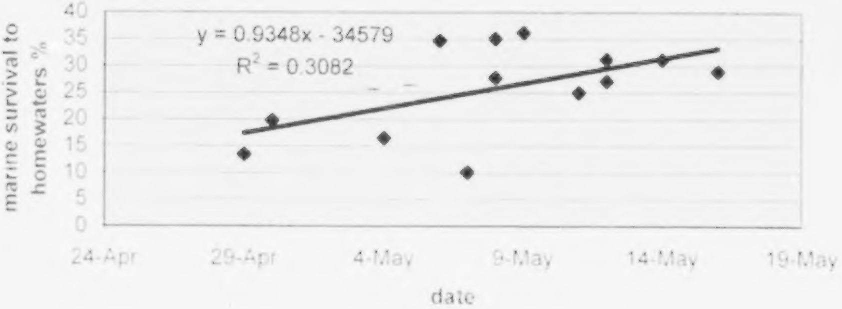

Figure 5. Marine survival (%) of River Bush 1SW salmon expressed as returns to Irish homewaters relative to median date of smolt migration.

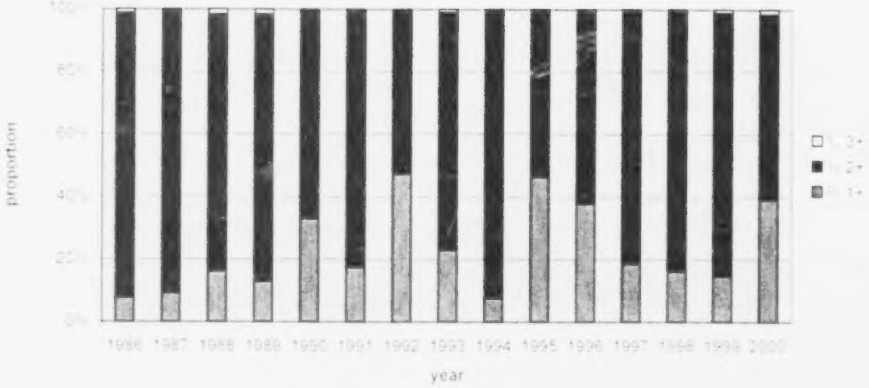

Figure 6. Proportions at age in the annual smolt run of River Bush Atlantic salmon.

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EFFECTS OF ENDOCRINE DISRUPTORS ON PARR-SMOLT TRANSFORMATION IN ATLANTIC SALMON (*Salmo salar L.*)

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BACKGROUND

We recently published a paper showing that past chemical use may have had an effect on wild Atlantic salmon (*Salmo salar* L.) populations in Atlantic Canada (Fairchild et al. 1999). We investigated the historical relationship between spraying in Atlantic Canada's forests and subsequent salmon returns to their local rivers over a ten-year period from 1975 to 1985. The concern was that during this time period, one of the insecticides sprayed, Matacil®1.8D, contained high concentrations of a compound called 4-nonylphenol (4-NP). From laboratory studies, these nonylphenols, which are classified as Endocrine Disrupting Chemicals (EDCs), are known to be toxic to invertebrates and fish and to have estrogenic effects. We found that for tributaries within one river, there was an association between the amount of Matacil®1.8D sprayed in 1977 and the number of salmon returning 2 years later. In addition, sixteen rivers in Newfoundland and New Brunswick exposed to spraying between 1973 and 1990 were evaluated, and the results indicated that a significant number of the lowest salmon catches coincided with Matacil®1.8D spraying. In 1980, Matacil®1.8D was phased out of spray formulations for New Brunswick forests and replaced with Matacil®1.8F, a compound that did not contain 4-NP. There was no significant relationship found between spraying Matacil®1.8F and salmon returns. The study also found a decline coinciding with the use of Matacil®1.8D and blueback herring catches in New Brunswick.

Matacil®1.8D was used as an insecticide to control damage from the spruce budworm. A single or repeated dose could be expected to reach many salmon streams between mid-May and mid-June, depending on the year and timing of the spray program which was aimed to match the local development of the spruce budworm larvae. After spraying, it is estimated that the concentrations of 4-NP in the water was in a range which was not sufficient to kill the salmon immediately but may have caused estrogenic effects on the salmon. What is unique about the Matacil®1.8D research is that there are very few examples where we can show effects of a chemical on wild fish populations. For EDCs, typically studies have focused on the reproductive system of fish. This study looks at the effects on smoltification and, although it has endocrine hormone involvement, the effects are not on the reproductive system of the fish where they might be expected. This study contributes to the understanding of EDCs and their effects in the environment.

While Matacil® 1.8D is no longer used in forest spraying, concentrations of 4-NP in the same range as those that were found in forest streams after spraying (20 µg/L) are currently found in discharges from sewage treatment plants and other industrial effluents (Bennie et al. 1998). These occur often as a breakdown product of nonylphenol ethoxylates (NPEs)(Bennie 1999). NPEs are used in household and industrial cleaning products, paints, pesticides, and in industrial processes such as pulp and paper, textile manufacturing, petroleum production and leather manufacturing (Blackburn et al. 1999; Sheahan et al. 2002). While many countries, including Canada, are looking at the levels of NPEs in the environment, an immediate solution or alternative is unlikely because of their widespread uses. Nonylphenols are on the Priority Substance List II of the Canadian Environmental Protection Act that will contribute to regulations on their future use (Hewitt and Servos 2001). For Atlantic salmon, if the mechanism of effect on smoltification is due to the estrogenic potential of 4-NP, then many other endocrine disrupting compounds encountered in the environment may also be important (Madsen et al. 1997; Moore et al. 2003).

To identify an outcome that may be predictive of adverse effects for migrating salmon populations, the present project aimed to verify whether parr-smolt transformation (PST) in Atlantic salmon is sensitive to the low levels of estrogenic and/or androgenic substances that may occur from current discharges into rivers supporting sea-run salmon stocks. To help estimate the risk from these discharges, the project assessed dose-response relationships to known estrogenic and androgenic substances. Most current sources of environmental steroids are from sewage effluents, agricultural wastes or industrial effluents, and the ability of these mixtures to produce effects similar to those observed for pure compounds will be evaluated. The experimental and field portions of the work were conducted in Atlantic Canada by Fisheries and Oceans Canada researchers from Moncton and St. Andrews, NB. Logistical and analytical support was supplied by Environment Canada researchers from the National Water Research Institute and by collaboration with scientists from the University of Manitoba and the University of New Brunswick. This project is complementary to other work investigating the fate and persistence of endocrine disrupters under other initiatives such as the National Municipal Effluent Strategy (CCME). The results are also relevant for risk management of alkylphenols under the current CEPA PSL II assessment. To improve predictive capability and understanding, potential mechanisms whereby estrogenic and androgenic substances exert their adverse effects on seawater adaptability and survival was be investigated. This represents a novel line of research examining an endocrine-sensitive developmental process (PST) that is critical to long-term growth and survival of salmon. Overall, the findings will contribute to understanding of factors that may affect sustainability and management of both Canadian and international stocks of Atlantic and Pacific salmon.

PROJECT OBJECTIVES

- To verify whether environmental levels of 4-NP and estradiol (E2) can affect seawater growth and survival of salmon. E2 provides a positive control for estrogenic effects.
- To identify critical temporal windows for exposure and determine threshold doses for these substances.
- To determine whether current discharges of endocrine disrupters (e.g., sewage and pulp mill effluents) into potential staging areas for salmon smolts are capable of impairing seawater growth and survival.
- To identify and understand mechanisms to improve predictive capacity for populations at risk.

BIOLOGICAL SAMPLING AND ENDPOINTS

Blood and tissue samples required for analyses were collected in the spring, summer and fall as per the field and laboratory exposure milestones associated with this project.

Measurements were made for three purposes: a) monitoring levels of test substances to determine the actual amounts to which fish are exposed; b) evaluating the performance characteristics (growth parameters, sea water survival and PST characteristics); and c) investigating parameters relating to potential mechanisms underlying the disruptive effects (endocrine and biochemical indices) that could lead to improved predictive capacity.

Plasma samples and tissue samples were immediately prepared upon sampling and stored at -80 ° C. Tissues were dissected for the various histological and biochemical measurements and carcasses were stored at -40 °C pending analyses. During the laboratory phases, daily records of feed intake as well as mortality and water quality parameters (dissolved oxygen content and salinity where applicable) were maintained. Six fish were removed from each tank/cage for each pre- and post-treatment sampling for a total of 12 fish per treatment at each sampling time. Tank and tissue levels of 4-NP were collected for determination by Selective Ion Monitoring GC-MSD. Water E2 levels were verified by specific enzyme immunoassay procedures following solid-phase extraction.

Biochemical, Histological and Endocrine Parameters. Samples collected for osmoregulatory parameters include plasma and tissue ions (Na^+, K^+ and Cl^-) gill Na^+/K^+-ATPase activity and gill chloride-cell histology. Samples collected to assess the role of various growth factors include plasma and tissues to assess GH & IGF-I , thyroid histological appearance, plasma thyroid hormone levels, and the activities of liver and brain deiodination pathways. Samples were collected for monitoring levels of E2 and testosterone and the egg yolk protein, vitellogenin, a commonly assessed biomarker for exposure to estrogenic substances.

Growth, Osmoregulatory Performance and Survival. The influence of test substances on fish performance was assessed on the basis of weight gain, specific growth rate (% increase in weight/day), condition factor, % survival, and ability to withstand sea water challenges.

LABORATORY EXPERIMENTS

Exposure Metrics. Measured 4-NP concentrations were 25-50 % of the targeted nominal concentrations of 20 and 200 µg/L, while E2 concentrations approached targeted nominal concentrations of 100 ng/L. This E2 aqueous concentration over a 5-day period would be expected to induce vitellogenin (see below). Concentrations of 4-NP in samples of smolts exposed to 4-NP in the laboratory experiments were determined. Whole fish tissue were found to range from the detection limit < 0.05 µg/kg to 38 µg/kg of 4-NP. In general, 4-NP exposed fish exhibited whole body bioconcentration factors near 300-500 folds of measured water levels.

Ionoregulatory Indices. Exposed smolts readily withstood seawater challenges and the altered plasma ion concentrations found following exposure of Atlantic salmon smolts to 4-NP and E2 in preliminary experiments was not confirmed in subsequent experiments. Analyses of plasma (Na, K, & Cl) and tissue (Na, K, and Cl) showed no treatment related effects. There was evidence that exposure to 4-NP and E2 caused increased muscle water content while in freshwater. However given that muscle and plasma ion levels were unaffected, changes were within the compensatory scope of ion exchange mechanisms. Gill Na,K-ATPase activity followed expected patterns associated with freshwater to seawater transfer. Preliminary experiments showed that high doses lowered gill Na,K-ATPase, however, this was not apparent with the low exposure doses used in 1999. Consistent with plasma and blood ions there were no treatment-related effects on gill Na,K-ATPase. Analyses of samples taken in 2000 are ongoing. Gill histology showed expected changes associated with seawater adaptation but evidence of treatment-related effects is pending more detailed measurements.

ELISA for Atlantic salmon Vg. We developed and characterized an indirect competitive binding ELISA for the measurement of vitellogenin (Vg) in plasma of Atlantic salmon. We also adapted gel electrophoresis and western blotting techniques for the confirmation of Vg in plasma of Atlantic salmon. We have completed analysis of Vg from the preliminary experiments and confirmed Vg levels in a selection of samples by PAGE and Western blotting. The Vg data clearly indicate exposure to estradiol and high doses of 4-NP in both sexes of fish.

Analysis of reproductive steroids. Analyses of reproductive steroids have been completed for all the samples collected. So far, plasma concentrations of estrogen and testosterone were very low and typical of immature fish. Estrogen levels showed some oscillations prior to seawater transfer but there were no treatment related differences following exposures to 4-NP. Consistent with induction of vitellogenin yolk-proteins plasma E2 levels were slightly elevated immediately following the freshwater exposures to E2. Plasma testosterone levels were more variable before both seawater transfers and subsequent grow-out but exhibited few treatment-related differences. Plasma testosterone levels were consistently higher in male relative to female salmon smolts but showed no relationships with growth rate.

Plasma cortisol, glucose and liver glycogen. Plasma cortisol measurements were initially low but showed a surge several weeks prior to seawater transfer that was typical of previous observations of cortisol dynamics during parr-smolt transformation. In early-run fish exposed to E2 during parr-smolt transformation cortisol was lower than in control fish but there were no treatment effects in fish exposed during mid or late run. Plasma glucose levels were typical of unstressed fish and tended to be slightly higher in females. Exposure of fish to 4-NP or E2 caused few consistent changes in glucose levels. Liver glycogen levels increased following sea water transfer but there were few treatment-related differences. Liver glycogen levels did not significantly differ between fish identified as fast or slow growing fish.

Thyroid status. Plasma levels of both circulating forms of thyroid hormones, thyroxine (T4) and triiodo-L-thyronine (T3) followed profiles typically observed during parr-smolt transformation. Levels peaked in February to May and declined in June before seawater transfer. Only fish exposed to E2 in early May exhibited depressed plasma levels of T4. Plasma T3 levels and thyroid gland histology were unaffected by the treatments. Changes in liver tissue T4 outer-ring (T4ORD) were consistent with previous studies in Atlantic salmon. Hepatic T4 inner-ring deiodination (T4IRD) and particularly T3 inner-ring deiodination (T3IRD) activities were much higher than those for T4ORD activity. Their activities peaked March to May but significant activity was also maintained in June during the final stages of smoltification. Both T4IRD and T3IRD activities were significantly inhibited after 2 weeks by exposure to E2 (100 ng/L). Only T3IRD was inhibited by the 4-NP exposures. Brain T3IRD activity is greater than T4IRD or T4ORD activities consistent with previous studies on Atlantic salmon. Both 4-NP (20 µg/L) and estradiol (100 ng/L) significantly depressed brain T4ORD but the T4- and T3IRD pathways were unaffected. In summary, these data confirm that changes in plasma thyroid hormones and deiodination activity in brain and liver are occurring during parr-smolt transformation, and that these activities are significantly altered by 4-NP (20 µg/L) and E2 (100 ng/L), with as yet undetermined effects on other aspects of smoltification.

Investigations on the growth hormone/IGF-1 axis. We tested a commercial RIA kit for IGF-1 and found it to lack suitable reliability. We then implemented an IGF-1 method based on that used by Dr. Penny Swanson from the NOAA Lab in Seattle, WA. The "Early" time-window was found to be the most sensitive time window for exposure of 4-NP and E2. Results from treatments beyond that time window suggest that the smolts had been held in fresh water too long and had begun to desmoltify. The results of this study suggest that the mechanism of action of 4-NP and E2 involves disruption of the GH/IGF-1 axis. Plasma IGF-1 may be a good predictive indicator of short-term water-borne exposure to steroidogenic substances during the final stages of PST.

Growth and Survival. Our laboratory experiments showed that growth, based on weight gain in treated salmon from transfer to salt water (mid-June) to October, was bimodal. This suggests that part of the population is affected by the treatments. By October, we were still able to observe a higher proportion of small fish resulting from exposure to either E2 or 4-NP. There were no treatment-related effects on survival immediately following exposure or during long term grow-out in sea water.

FIELD EXPERIMENTS

Exposure metrics. Analyses of the trace metal and polycyclic aromatic hydrocarbon (PAH) content of water and sediment from the Miramichi have been mostly completed. PAH levels in river water were mostly below detection. Pulp mill effluent contained anthracene above Canadian Water Quality Guidelines (CWQG) and sediments at Chatham contained PAH levels exceeding Canadian Interim Sediment Quality Guidelines (CISQG) but below Probable Effects Level (PEL). Numerous trace metals (Al, Ba, Be, Co, Cr, Cu, Fe, Li, Mn, Mo, Ni, Pb, Sr, Ti, V, Y, Zn) were detectable. Trace metal analysis shows ion and nutrient enrichment in pulp mill and sewage effluents. Highest metal levels were in pulp mill effluent and nearby water where Cu, Al and Cr consistently exceeded CWQG. Sediment Cr and As consistently exceeded CISQG and some cases were above PEL. NP concentrations in smolts collected from the Miramichi River were below detection limits. Water and sediment samples collected from the Miramichi estuary had low concentrations of NP. However, there was low level yeast estrogen screen activity and detectable estrogen levels associated with sewage inputs along the left side of the estuary.

Growth and Survival. Wild smolts collected upstream in the NW Miramichi were caged at various locations in the Miramichi and in Tabusintac (control) estuaries. Bimodal growth patterns were evident in fish regardless of caging site. However, relative to the fish caged at the Tabusintac reference site, the proportion of small fish was significantly greater for the fish caged at three locations in the Miramichi estuary. There was no difference in the proportion of big and small fish among the upstream and downstream caging sites in the Miramichi. The upstream site was located near a potential source of agricultural waste input near Cassilis and the downstream sites at Strawberry Point and Old Ferry Road experience influence from domestic sewage and pulp mill effluent.

ECOLOGICAL SIGNIFICANCE OF IMPAIRED GROWTH

Marine survival of given smolt year classes were strongly correlated with early ocean growth as estimated by measuring the spacing of scale circuli on returning adults (Holtby et al. 1990). It was thought that size selective predation was the possible driver for the relationship between relatively fast growth and relatively high survival. In a scale circuli study of the first sea-year in Atlantic salmon, it was found that growth during the first winter may be critical to smolt survival of North American stocks (Friedland et al. 1993). The relationship between selected measures of smoltification and subsequent adult returns were examined for four groups of hatchery reared chinook salmon (*Oncorhynchus tshawytscha*) in the Deschutes River, Oregon (Beckman et al. 1999). Only spring growth rate, gill ATPase activity and plasma IGF-1 showed significant relationships to smolt-to-adult return. These characteristics were also consistently lower from sites with lower adult returns than from better performing sites. The authors concluded that differences in the quality of the smolts released by hatchery facilities may have profound effects on subsequent survival. Atlantic salmon smolts exposed to steroidogenic substances in our laboratory experiments have a greater proportion of slow growing individuals, and a higher proportion of individuals with lower plasma IGF-1 values in the months after introduction into seawater. Smolt characteristics may also be predictive of smolt-to-adult return in Atlantic salmon, as has been demonstrated by Beckman et al. (1999) for hatchery reared chinook salmon. If true, then exposure to low levels of steroidogenic substances can produce Atlantic salmon smolts with characteristics (growth and IGF-1) consistent with smolts having a lower expectation of returning as adults.

CONCLUSIONS

- Aqueous exposure to 4-NP, estradiol or testosterone in the lab altered various biochemical parameters some of which were indicators of exposure (E2/Vg) and identified others which may be predictive of effects (e.g. T_3, deiodinase and IGF).
- 4-NP, estradiol and testosterone exposure in the lab affected subsequent growth in seawater in up to 40% of exposed fish.
- We have identified the potential for a critical temporal window for exposure.
- Low levels of several endocrine disruptors associated with effluents impaired sea water growth.
- When Atlantic salmon were caged in the Miramichi River in 2000 there was a greater proportion of small fish in August relative to those held at a reference location.
- Chemical analysis of Miramichi water revealed low levels of several factors that may be capable of affecting subsequent seawater growth. However, further work is necessary to identify causative agent(s).

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10

LINKS BETWEEN ENVIRONMENT, GROWTH AND SURVIVAL IN ATLANTIC SALMON (*Salmo salar* L.) AND THE IMPLICATIONS FOR MODELLING PREFISHERY ABUNDANCE

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INTRODUCTION

There are numerous factors that affect survival of Atlantic salmon (*Salmo salar* L.) in the marine environment, abiotic as well as biotic, and the interactions between them are poorly known. Understanding how environmental factors influence marine survival is crucial to explaining the variability seen in the recruitment of Atlantic salmon. However, the task is complex and many factors are likely to be acting together, in some combination, to influence the level of survival. The mix and contribution of individual factors will also be likely to vary depending on, for example, location, life stage, and genetic predisposition of different stocks/populations.

Marine mortality of Atlantic salmon varies considerably among stocks and years, but is lowest for salmon that have spent one winter at sea. Many factors affect the survival (Ritter 1989), although they are generally poorly understood (Friedland and Reddin 1993; Reddin and Friedland 1993). Some of these factors are outlined in Fig. 1. The parr-smolt transformation (smolting) and the post-smolt stage (the period just after the smolts have left the rivers) are of particular interest because these periods may be critical for survival in the sea (McCormick et al. 1998). Friedland et al. (2000) showed that postsmolt growth was enhanced in years with favourable temperature conditions, which in turn resulted in higher survival rates.

This paper aims to summarize some major sources of mortality of salmon at sea, with main emphasis on links between the marine environment, growth and survival in relation to prefishery abundance (PFA) modelling.

FRESHWATER INFLUENCES

The timing of smolt migration seems to be crucial for survival of Atlantic salmon (Hansen 1987), and the development of an optimal period of emigration (sometimes referred to as the "smolt window") is presumably an adaptation to the area's prevailing environmental conditions. This may be related to interaction between environmental factors and physiological processes (McCormick et al. 1998). In addition to the change in physiological state of smolts, it is likely that there are other mechanisms behind the observations that there is an optimal time for smolt migration. These are less well understood, but predators, diseases, parasites and food conditions clearly contribute to smolt mortality. The survival window has been suggested to be open for a few weeks during spring and gradually closes during the summer (Larsson 1977; Hansen and

Jonsson 1989). In Norwegian rivers draining areas with high snow fall, the current velocity and turbidity increase considerably during snow melt. Survival of hatchery-reared smolts in the Gaula and Surna rivers increased when they were released at high water discharge within the normal period of migration (Hvidsten and Hansen 1988). Survival may have been improved because the smolts move close to the water surface and descend more quickly at high current velocity, and they may be less vulnerable to predation owing to the high turbidity.

One important example of freshwater related marine mortality is the effect of acidity and aluminium on smolt development. It has been known for some time that acid (and acid plus aluminium) exposures that have little effect on survival and growth of parr or smolts in freshwater can completely eliminate the development of gill Na^+, K^+-ATPase activity and salinity tolerance (Saunders et al. 1983). Exposures as short as 12 h to relatively mild acidity with high aluminium levels can compromise salinity tolerance (Staurnes et al. 1996). There are also other pollutants in freshwater that may result in reduced salt water tolerance of smolts (Fairchild et al. 2003).

Other freshwater effects have also been linked to variation in marine survival. Ricker (1962, 1976) demonstrated that, in sockeye salmon, smolt size was positively related to survival. Koenings et al. (1993) found that survival varied with the latitude of the nursery stream. This particular study illustrates the difficulty in highlighting the causal factor, as an equally plausible explanation would be the sea conditions upon entry to the ocean.

FOOD

Food availability is an obvious candidate as a driving force in determining marine survival but, as yet, its importance has not been demonstrated. Survival of post-smolts may be connected with abundance of suitable prey, particularly during the period immediately after they leave freshwater. When the smolts enter saltwater their expenditure of energy increases (Farmer et al. 1978), and scarce food resources may result in increased mortality. Lack of food would also reduce growth rate and increase their vulnerability to size-selective predation.

The frequency (by volume) of the main prey groups taken by post-smolts in a Norwegian fjord area just inside the open coastal zone showed great temporal variations, e.g. insects dominated the first two years and crustaceans the third year (Hvidsten et al. 1995). There were also spatial variations within a year, e.g. in 1994 euphausiids dominated in the fjord area, whereas farther out the importance of this group was somewhat reduced, as amphipods (Hyperiidae) and fish (herring larvae) became important as well. This pattern was further confirmed by Andreassen et al. (2001) and they pointed out that the gradual change in diet suggested that feeding conditions in the early marine phase were important for survival and growth of the post-smolts.

The feeding habits of post-smolts have been analysed in the area west of the British Isles and in the Norwegian Sea (Holst et al. 1993; 1996). The proportion of empty stomachs was relatively small (3-15%), which might indicate favourable feeding regimes in the sampled areas (Holst et al. 1996). Results of post-smolt trawls in the Norwegian Sea have indicated that at this early stage of ocean life food is plentiful (Shelton et al. 2000).

GROWTH

Salmon grow relatively fast in the sea, but the plasticity of salmon growth makes the discrimination between the extent of genetic and environmental influences difficult. Differences in growth rates could, for example, be due to variable food supply, or more general changes in oceanographic processes and structural features in the water column (Levings 1994). These changes might affect some populations more than others, depending on their marine distribution. Differences in growth rates may also be shaped by patterns of natural selection in individual rivers. Jonsson et al. (1991) observed that Atlantic salmon in rivers with annual average flows of less than 40 m^3s^{-1} were smaller than salmon in larger rivers, and suggested that selection in small rivers may act against large salmon because low water flows make successful ascent and breeding by large salmon risky and difficult. Mortality of salmon at sea and fish size has been hypothesised to be inversely related (Doubleday et al. 1979). Friedland et al. (2000) found a significant relationship between sea surface temperatures and observed survival, and that the back-calculated growth in the first sea year varied between 32 and 43 cm in the period 1965 to 1993. High growth-rates were associated with high temperatures, which in turn resulted in higher survival rates (Fig. 2). However, the results of the study on the River Bush show no link between marine survival and growth suggesting that factors other than, or in conjunction with, growth determine survival (Crozier and Kennedy 1999) for this particular stock.

COMPETITION

In the Norwegian Sea, Norwegian spring spawning herring (NSSH) and mackerel are also present at the same time as post-smolts (Holst et al. 1996). Herring larvae may be important food for post-smolts in coastal areas, but adult herring and mackerel may be competitors in the ocean. The biomass of herring has increased considerably in recent years, and thus it is reasonable to ask if this may affect growth and survival of post-smolt salmon. Some preliminary information may support the hypothesis that the presence of large numbers of Norwegian spring spawning herring in the Norwegian sea may contribute to increased mortality of salmon in the ocean. This is indicated by an observed negative relationship between herring abundance and salmon catch, as well as between herring abundance and marine survival of smolts from the River Figgjo. However, the quality of the time series are variable, and in some cases estimates have been used without taking consideration of the fact that there may be considerable variation among the variables.

PREDATION

Predation is probably the most important source of mortality, and diseased fish are likely to be eaten before they perish. Anthony (1994) discussed predatory birds, fish and mammals as sources of marine mortality in salmon. The main predation is believed to take place at the post-smolt stage, the first months after the smolts leave their home rivers. This is based on the assumptions that small fish are exposed to a larger range of predator species than large fish, and that there are more predators inside the continental shelf than in oceanic areas.

Quantitative information on predation in the ocean is scarce but it has been speculated that sharks and skates may eat salmon, and there is some documentation of consumption by seals and whales (Pierce et al. 1991; Shearer 1992; Hislop and Shelton 1993).

Predation on smolts and post-smolts may be most severe in estuaries and fjords, just after the smolts have left freshwater. In the estuaries of the River Surna and River Orkla, Norway, heavy predation by fish, mainly cod, has been observed on both hatchery-reared and wild smolts (Hvidsten and Møkkelgjerd 1987; Hvidsten and Lund 1988). Reitan et al. (1987) showed that many migrating hatchery reared smolts were eaten by sea birds.

Although not directly associated with predation, high levels of sea lice have been reported to cause mortality on post-smolts in local environments (Finstad et al. 2000).

ENVIRONMENT

The decreased Atlantic salmon abundance in recent years has been most pronounced in North America, although there is also a significant decrease in Europe, particularly in southern areas. The decline is more pronounced for MSW salmon than for grilse, suggesting that changes in the marine environment may affect the survival of salmon in the sea (e.g. Ritter 1989). Friedland et al. (1993) showed that interannual variation in the area of potential post-smolt habitat at sea, defined as the area combining their optimal temperature and full marine salinity, is significantly correlated with catches of salmon from this area. Further studies, using time series of smolt survival rates, seem to confirm this.

If the driving force behind marine mortality is temperature-related, one might predict that survival of salmon stocks migrating as post-smolts into the same area would be correlated. This hypothesis was tested using time series of survival estimates of wild salmon from the River Figgjo, Norway and the North Esk, Scotland (Friedland et al. 1998, 2000). These rivers enter at opposite sides of the North Sea at about the same latitude and salmon from both rivers have been observed in the Faroes fisheries at the same time. Hence it was assumed that both groups are subjected to the same marine environment for at least the first months at sea (both stocks migrate to sea in early May). Return rates of 1SW and 2SW salmon from Figgjo were significantly correlated, as were 1SW and 2SW salmon from the North Esk, supporting the hypothesis that most mortality takes place in the first year at sea. Furthermore, there were significant correlations in return rates between salmon from both rivers, suggesting that survival was driven by common marine factors (Fig. 3). A positive correlation was found between the area of 8-10° C in the Norwegian Sea north of the outlet of the respective rivers in May and the survival of salmon, which supports the hypothesis of temperature-related mortality in the sea (Fig. 4).

Changes in marine environments may change the life history of salmon. A changed climate may for example change the timing of smolt migration. There is an apparent optimal sea temperature at post-smolt entry. If temperatures in the freshwater and marine environments are not synchronised, this may affect the mortality of post-smolts (Crozier and Kennedy 2003; Dempson et al. 2003). For example, if temperature increases in freshwater, the smolts may be triggered to migrate to sea earlier. But if the sea temperature has not changed, or has decreased, this would result in the smolts moving into an environment that is not optimal for them.

A changed marine climate may also affect growth rate and thus sea age at maturity. Hutchings and Jones (1998) found a positive correlation between sea-age at maturity and growth rate at sea for Atlantic salmon, as was also observed by Jonsson et al. (2002). Thus a faster growth in the marine environment may produce salmon of older sea age.

Climatic variations play a major role in shaping the marine environment and can influence currents, gyres and SSTs (sea surface temperatures). Such changes may impact upon salmon directly through altering factors influencing migration routes or indirectly by shifting the distribution, and/or quantity, of food availability at one or several levels in the oceanic food chain. Furthermore, sea temperature may also determine abundance and distribution of potential salmon predators and competitors. Temperature is also a key factor for the physiological metabolism of salmon, and thus affects growth rates.

Evidence that such effects could be relevant are described by Holm et al. (1996) and Shelton et al. (1997) who found that the distribution of post-smolts was associated with strong currents. However, both Hansen et al. (1993) and Reddin and Lear (1990) report that returning adult salmon appear to approach natal rivers independently of prevailing currents indicating that the effects of environmental factors can, in some cases, act specifically at certain stages of the salmon's life cycle.

The recent changes in the NAO index (a measure of the difference in atmospheric pressure between a northern and southern area of the North Atlantic) to extreme positive states has led to increased interest in how such changes impact upon growth and survival in Atlantic salmon. It has been shown that a strong positive correlation exists between the NAO and indices of salmon. The NAO can influence temperature, wind strength, salinity and wave height, all factors that could have effects on recruitment through a range of mechanisms at different stages of the salmon's life cycle (including freshwater effects) (Dickson and Turrell 2000).

IMPLICATIONS FOR MODELLING PREFISHERY ABUNDANCE

Our current concepts of variation in natural mortality (M) have been influenced by the proposal by Doubleday et al. (1979) that an inverse weight model, whereby the rate of mortality would be negatively related to fish size, was intuitively rational for Atlantic salmon. A similar model has been used by Furnell and Brett (1986) to analyse growth and mortality parameters in sockeye salmon. Fitting this model to a few stocks/populations has led to an acceptance that most mortality occurs in the early marine phase and that after the first winter in the ocean M is approximately 0.01 per month. While M may vary around this accepted average value in the months between recruitment and return to freshwater, and also among stocks, it has been shown that at this approximate level the sensitivity of the current PFA model output to changes in M is low (Potter et al. 1998).

Factors affecting the marine survival of salmonids in the early marine phase include ocean productivity and growth related predation factors (eg. Holtby et al. (1990) in Pacific salmon and Salminen et al. (1995) in Baltic salmon). Consequently, most research into marine survival has focused on this early phase. For example, Friedland and Reddin (1993) suggested that, on the basis that return rates to geographically separated stocks in North west Atlantic showed similar patterns, common oceanic conditions were being experienced by all stocks. Similarly, on the European side, Friedland et al. (2000) have investigated the relationship between trends in marine survival with respect to SSTs and growth parameters. The initial observation is that return rates to two geographically separated monitored rivers, the Figgjo in Norway and the North Esk in Scotland, show a significantly similar patterns. Furthermore these return patterns correlate with SSTs derived for the oceanic area thought to be utilised by post-smolts from both countries. Evidence that the post-smolt phase is important comes from the observation that post-smolt growth increments for the North Esk stock also correlate with return rate. While the mechanisms influencing return rate are unknown, the correlation with growth points to growth mediated mechanisms.

To date, the modelling attempts for the Northeast Atlantic area (NEAC) have largely been limited to describing past levels of PFA (ICES 2001). Catch advice has been based, partly, upon a forward extrapolation of the trend in the PFA values for 1SW and MSW salmon separately. A more powerful model would be one that had a predictive element, similar to that used in the North American run reconstruction model (ICES 2001), that would allow forecasts of PFA for the NEAC area to be made based on some indicative environmental/biological variable.

The link between SSTs at the post-smolt stage and survival to homewaters at the adult stage opens up the possibility of incorporating a predictive element into the PFA model. To develop such an approach, the first step would be to determine to what extent the variables (SST, growth, and survival) discussed above correlate with outputs from the PFA models. Secondly, the spatial and temporal boundaries with respect to stock cohesiveness, in terms of growth patterns, and environmental correlates need to be defined. The large number of archived scale data sets that exist throughout the NEAC area (ICES 1999) could be utilised for this purpose. Studies aimed at assessing the cohesiveness of growth signatures at a regional level have already begun in England and Wales, Scotland and in Northern Ireland.

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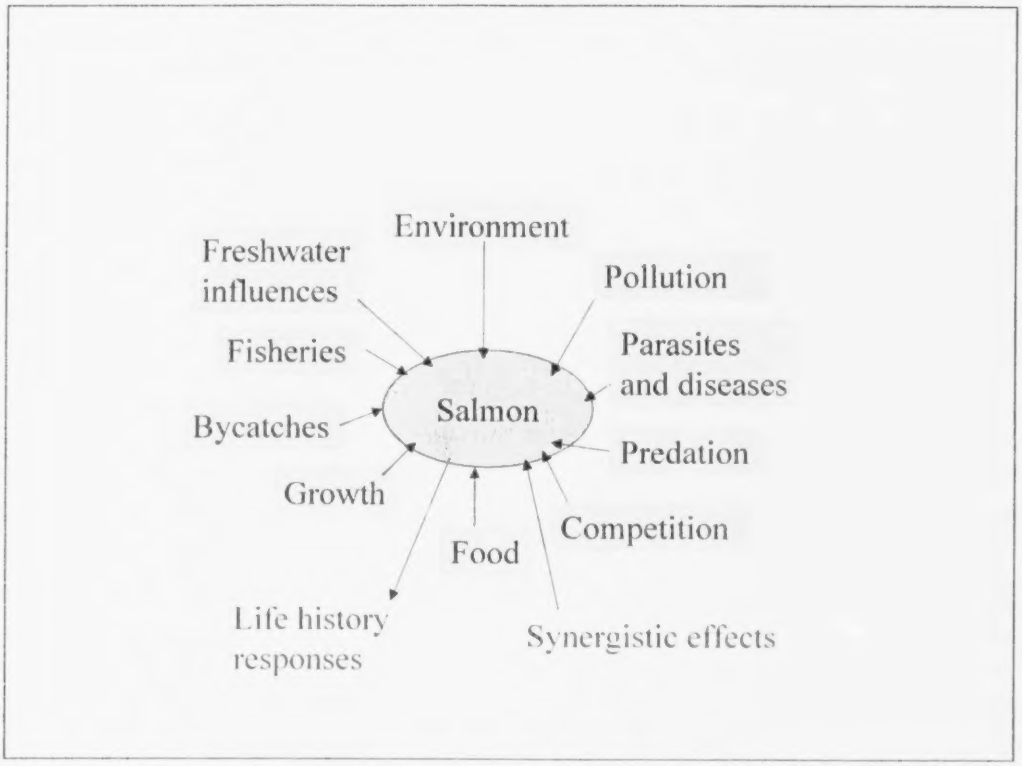
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Pollution
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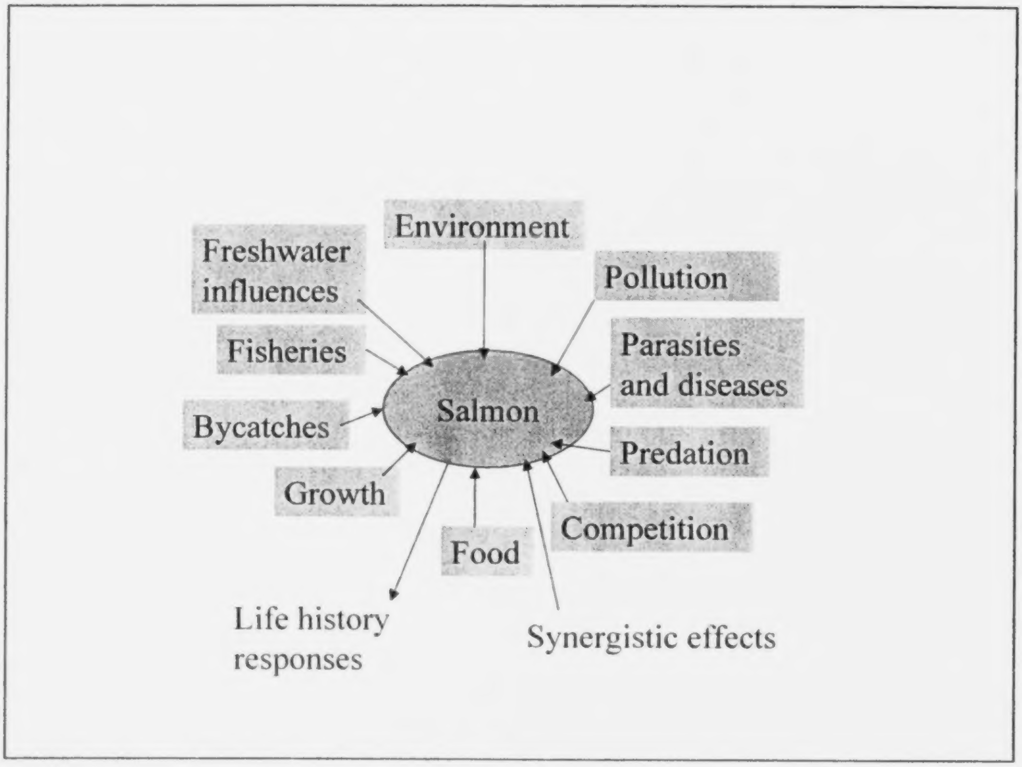
Parasites and diseases
Salmon
Bycatches
Predation
Growth
Competition
Food
Life history responses
Synergistic effects

Figure 1. Potential mortality factors for salmon in the sea.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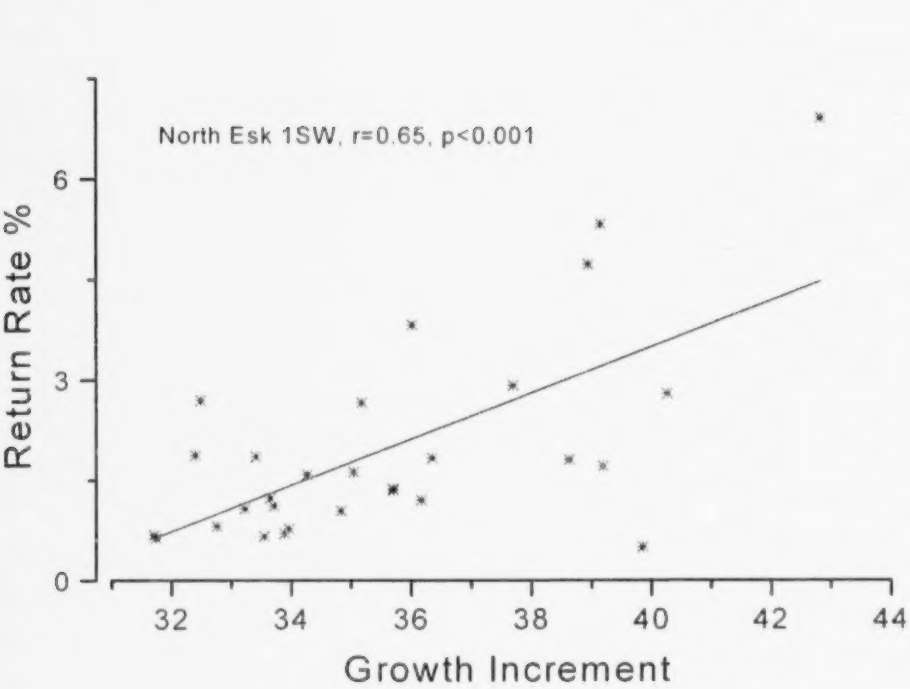

Figure 2. Scattergram and regression between 1SW return rate and post-smolt growth increment. Dashed line represents 98% confidence interval (from Friedland et al. 2000).

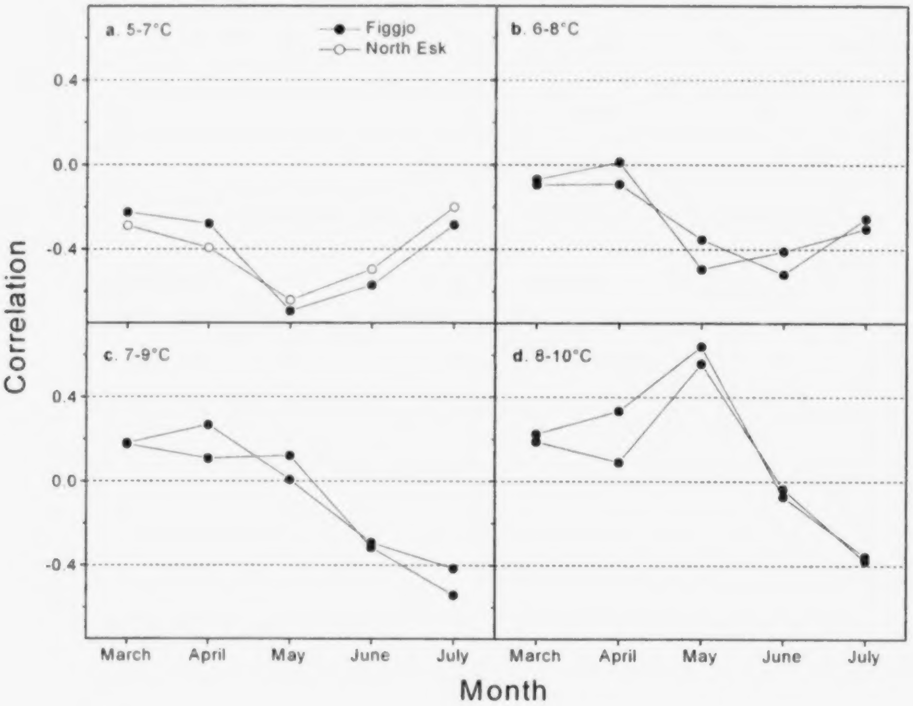

Figure 3. Correlation between 1SW return rate for Figgjo and North Esk salmon and thermal habitat versus month. Thermal habitat computed for four thermal ranges: 5-7°C (a); 6-8°C (b); 7-9°C (c); and, 8-10°C (d). Grid lines at r=0.4 represent the approximate location of significance at p=0.05 (from Friedland et al. 2000).

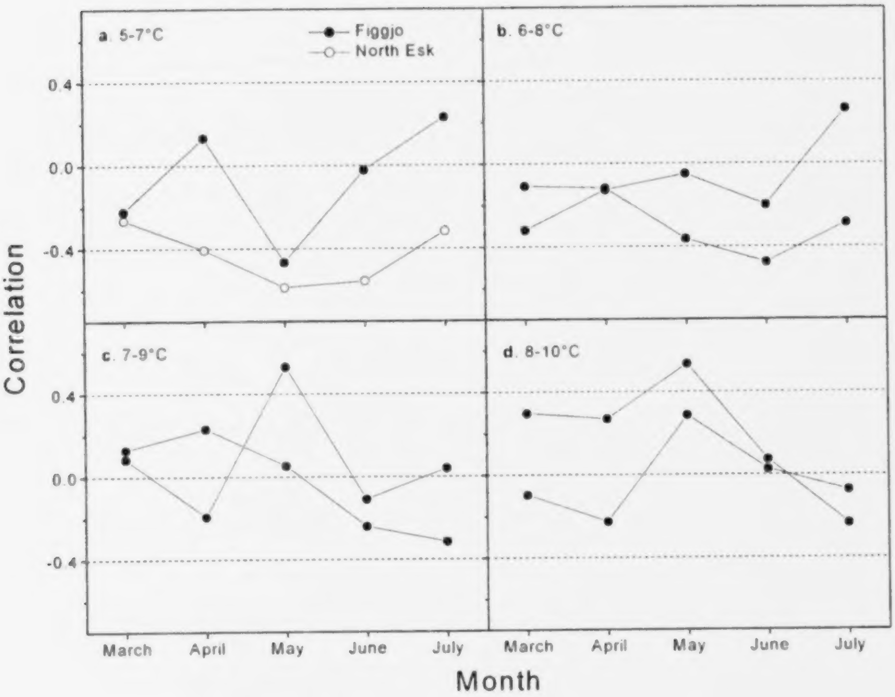

Figure 4. Correlation between 2SW return rate for Figgjo and North Esk salmon and thermal habitat versus month. Thermal habitat computed for four thermal ranges: 5-7°C (a); 6-8°C (b); 7-9°C (c); and, 8-10°C (d). Grid lines at r=0.4 represent the approximate location of significance at p=0.05 (from Friedland et al. 2000).

11

TEMPERATURE-MORTALITY RELATIONS IN MARINE-PHASE ATLANTIC SALMON (*Salmo salar* L.): THE SEARCH FOR UNDERLYING MECHANISMS

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INTRODUCTION

The prospect of major shifts in water temperature regimes due to global climate change has focussed attention on temperature-based limits to faunal distribution (Frank et al. 1990; Beamish 1995; Eaton and Scheller 1996; Drinkwater 1997, 2000; Dempson et al. 2001). Typically, these studies infer temperature preferences or limits from current distributions, and then predict new distributional limits under projected climate change regimes.

Recent declines in estimated pre-fishery abundance of Atlantic salmon (*Salmo salar* L.) in the Atlantic Ocean (ICES 2000) have heightened interest in possible relations between marine climate and marine mortality. Correlations have been reported between indices of salmon abundance and an index of nursery habitat area that is based on seasonally varying windows of temperature suitability (Friedland et al. 1993). Salmon abundance has also been reported to be linked to the area of the cold intermediate layer on the Newfoundland Shelf (Narayanan et al. 1995). Friedland et al. (2000) reported that North Sea salmon survival was associated with years of higher sea surface temperature (SST). However, links between temperature and marine survival of salmon in the Northwest Atlantic appear to have broken down in recent years, as temperatures in the Labrador Sea have increased while salmon continue to fare poorly.

Considerations of the biological effects of climate change and temperature effects on sea survival of salmon are largely empirical in approach. Salmon, like other fish, have lethal temperature limits which are physiologically determined. Salmon can tolerate waters from just below 0°C to 30°C (MacMillan 1998). Lethally cold temperatures can be avoided by diving to deeper water, and temperatures near the upper lethal limit are rare in the Northwest Atlantic. This means that direct lethality of temperatures is unlikely to control distribution or survivorship of salmon in the sea. Instead, we must look to the ecological effects of temperature. If we understand how temperature affects the way salmon interact with their environment, we will have a better chance of finding sustainable statistical relationships between marine climate variables and salmon survival at sea, and of creating reliable predictions of biological effects of climate change.

This paper develops a general model of the relation between temperature and marine community structure, and applies some of its features to Atlantic salmon in the Northwest Atlantic.

ENDOTHERMY, ECTOTHERMY, AND THE STRUCTURE OF MARINE COMMUNITIES

The structure of marine trophic webs changes dramatically with global latitude (Fig. 1) (Lavigne et al. 1989). In polar systems, small fish are preyed on by seals and pursuit-diving seabirds, which dominate the biomass of medium and large size-classes. Medium-sized fish are uncommon. At boreal latitudes, seals and pursuit-diving seabirds are common, but large fish (e.g. cod) are also present in large numbers. In temperate latitudes, seals and pursuit-diving seabirds are uncommon. In the tropics these predators are generally absent and the role of large predators is chiefly filled by sharks and other large fish. This pattern cannot be explained by the distribution of productivity because seals and pursuit-diving seabirds are absent from many tropical areas which are highly productive (Berger and Wefer 1991).

I propose that, in endotherm-ectotherm predator-prey systems, susceptability to predation is influenced by temperature, and that this is the key mechanism which explains global variation in the structure of marine predator communities. The ability of a fish to escape a predatory attack depends on its reaction time and swimming performance. In aquatic ectotherms, performance of nervous and muscular systems is strongly influenced by ambient temperature (Fig. 2) (Lin and Regier 1995). Although cold-water fishes have biochemical adaptations that mitigate temperature effects on enzyme systems, burst speeds and reaction times decline steeply with temperature (Johnston et al. 1991). Ambient temperature has little effect on swimming performance of marine endotherms because internal temperature is fairly constant.

This means that susceptibility to capture depends on the differential between water temperature, which determines internal temperature in ectotherms, and body temperature of the endothermic predator. Where this difference is large, such as in polar waters, the endothermic predator will have a major advantage over ectothermic prey. Where the difference is small, such as in the tropics, endothermic predators will have little advantage over ectothermic prey.

Temperature influenced susceptibility to predation effects should be greatest where predators detect and pursue prey in open waters. In such situations, the major determinant of attack success should be the speed and maneuverability of the predator vis-à-vis that of the prey. The effect should be less where predators surprise their prey at close quarters, so that the prey has little or no time to react. This would occur where predators search for prey that is hidden or immobile in vegetation or on the bottom (e.g. bottom-feeding cormorants feeding on flatfish). It would also occur where predators use gravity to enter the water at great speed, thereby surprising surface-dwelling fish (e.g. gannets plunge-diving for mackerel).

Most seals pursue prey in open water. In the Northern Hemisphere most pursuit-diving seabirds are members of the Alcidae family, which includes murres and puffins. In the Southern Hemisphere penguins are the main group of pursuit-diving seabirds.

On a global scale, the inverse relation between abundance of seals/pursuit-diving seabirds (abundant in cold water, rare in warm water) and abundance of large predatory fish (rare in cold water, abundant in warm water) is consistent with the hypothesis that temperature influences susceptibility to predation.

In the late 1980s and in the 1990s, there were major biotic changes in the Northwest Atlantic, particularly in the area of the Newfoundland Shelf. These changes included an influx of polar cod south to the Newfoundland Shelf (Lilly et al. 1994; Lilly and Simpson 2000) an influx of capelin south to the Scotian Shelf (Frank et al. 1996) rising seal populations (Stenson et al. 1999) and collapsing stocks of medium-size fish, notably cod (Myers et al. 1997). The changes in the Newfoundland Shelf marine community can be viewed as a shift from a typical boreal structure (moderate abundances of both marine endotherms and medium-sized fish) in the direction of a typical Arctic structure (marine endotherms are abundant, medium-sized fish are uncommon).

Summer surface temperatures on the Newfoundland Shelf dropped sharply in the early 1990s (Fig 3). Could a temperature influenced susceptibility to predation have contributed to the shift in community structure by enhancing predation by endothermic predators on ectothermic prey? It is clear that susceptibility did not initiate these changes, because the groundfish collapse was well underway before the drop in temperature, and the increase in seals was part of a long-term trend. Whether predation was influenced sufficiently to provide an advantage to seals and a disadvantage to fish in the cold years of 1991-1993 cannot be answered with present data.

During the winters of 1997-1998 to 1999-2000, there were numerous reports of seals biting pieces out of the bellies of cod in inshore Newfoundland waters (Lilly et al. 1999, 2001). The "belly-biting" phenomenon would be a manifestation of the influence of temperature on the susceptibility to predation if the seals' ability to approach their prey was due to the lowered swimming performance of cod induced by cold water. However, the circumstances surrounding these incidents are poorly known, and it is unclear whether factors other than low temperature may have contributed to the vulnerability of cod to seal attacks.

TEMPERATURE AND SALMON SURVIVAL

Atlantic salmon have much higher growth rates and much lower survival rates than other pelagic fish of the Northwest Atlantic (Cairns 2001). This suggests that marine-phase salmon take a "damn the torpedoes" approach to foraging, trading off high growth against high mortality. Salmon are also anomalous because they occupy northern areas (e.g. Greenlandic waters) where medium-sized fish are uncommon. Greenland cod and Arctic char are of the same size range, but have much slower growth rates, and presumably feed much less aggressively than salmon.

Atlantic salmon are susceptible to seabird predators during some or all of the post-smolt stage, and to seals during their full life at sea (Cairns and Reddin 2000). These endothermic predators are present throughout the range of salmon in the Northwest Atlantic. This suggests that temperature-dependent predation susceptibility could be a significant factor in the life of marine-phase Atlantic salmon.

The main factors in the demography of salmon at sea are temperature, food supply, growth, and mortality. Growth is primarily based on temperature, food supply, and foraging intensity. Predation is presumed to be a major or the major cause of mortality, although this is not known with certainty. Animals presumably attempt to make behavioural choices that result in a combination of growth and mortality that maximizes fitness. Because growth and mortality operate as trade-offs (Anholt and Werner 1995, Sogard 1997) it is not possible to simultaneously maximize both.

In some fish, growth rates show dramatic differences over time or among regions (e.g. Atlantic cod, Brander 1995). In Atlantic salmon, growth rates appear to be remarkably uniform. Coefficients of variation of mean fork length of adult salmon returning to the Miramichi River were only 3.7% for 1SW fish and 2.2% for 2SW fish between 1971 and 1999 (data from G. Chaput, Table 1). Mean weights of returning 1SW and 2SW adults had CVs of 5.0% for 1971-1991. In contrast, sea survival in salmon returning to particular rivers is highly variable, with CVs ranging from 20.6% to 58.3% (Table 1). The uniformity of return sizes suggests that salmon have a specific target size at return, which they achieve by adjusting their foraging intensity. Inter-year differences in foraging intensity lead to inter-year differences in mortality risk, which results in high variability of survival rates.

Little is known about the foraging behaviour of salmon at sea. Research and commercial fishing show that salmon commonly occupy the surface layers of the ocean (Reddin and Shearer 1987, Dutil and Coutu 1988). Recently, data from temperature loggers (Sturlaugsson 1995; Reddin et al. 1999) have shown that salmon undertake vertical migrations at times rapid, between the warm surface layer and waters under the thermocline. We can surmise that these movements are related to feeding, and also to the occupancy of warmer water which enhances growth. Salmon will increase growth by more actively searching for food and increasing the time spent in warm water. Diving beneath the thermocline may be necessary to increase growth if that is where the food is, but the fish will return to the warm layer when not directly involved in feeding because the warmer water will promote growth.

Little direct information is available on behavioural interactions between salmon and endothermic predators. If detection by predators is visual, then detection risk will increase with foraging intensity, because an actively moving salmon will more likely swim into the predator's visual field than one which is immobile. Detection risk will also depend on the thickness of the layer of water which the salmon normally occupies. When the warm surface layer is thick, there is more opportunity to stay at a greater depth where light is dimmer and chance of detection is lower, without sacrificing the warm ambient temperature needed to promote growth.

Observations of harbour seals and sea lions attacking chinook salmon in British Columbia bays indicated that the pinnipeds typically approached the salmon from underneath, and attempted to grasp the fish by the throat or belly (Bigg et al. 1990). Salmon were also observed rapidly swimming with sudden turns, with a pinniped in close pursuit. It seems reasonable to assume that outcome of such attacks would be influenced by temperature, which alters the salmon's speed and reaction time.

Chance of escape would also be influenced by the depth of the salmon when the attack begins. A salmon that is attacked from below while deep in the water column will have more room to swim up and away from its attacker than one that is near the surface. If salmon prefer to stay within the warm surface layer for growth promotion or other reasons, the thickness of this layer may have an influence on predation risk. When the warm surface layer is thick, salmon have the option of staying at a deeper level where predation risk is lower, but when the warm surface layer is thin, they are constrained to near-surface levels where predation risk is higher.

Table 2 summarizes the major interactions that are hypothesized to occur among salmon growth, mortality, and environmental conditions. In the absence of any behavioural response to environmental change, decreases in temperature, surface layer thickness, overall food supply, and food supply within the warm surface layer should depress growth and increase mortality. Salmon respond to these changes by increasing foraging activity, including dives beneath the thermocline. These have the effect of neutralizing impact on growth, at the expense of raising mortality.

The mechanism by which low temperatures increase mortality is twofold. First, low temperatures depress metabolism and therefore growth, so the fish need to feed more actively to maintain their target growth trajectories. The higher activity will lead to greater predation risk and therefore mortality. Secondly, the lower water temperature increases probability of capture by an endotherm attacker due to temperature influenced susceptibility to predation.

If the relations in Table 2 accurately mimic the life of salmon at sea, then we can expect negative relations between mortality and sea surface temperature, thickness of the warm surface layer, food supply, and food supply within the warm surface layer. We should also see positive relations between predator numbers and mortality. Growth and temperature, and growth and food supply, should not be correlated to any substantial degree because salmon adjust their foraging intensity to ensure that growth rates are nearly constant.

Amiro (1998) reported a negative relation between harp seal numbers in the Northwest Atlantic and sea survival of salmon. This is consistent with model predictions. Correlations between temperature and salmon success at sea have been found but relations have not proven to be consistent through time (Potter and Crozier 2000). No statistical relations between food supply and mortality have been documented (Jacobsen and Hansen 2000).

The concepts put forward in this paper could be examined through a combination of correlational analysis and experimental tests. There have already been tests of SST vs. sea survival. The relation between survival and thickness of the warm surface layer, or a thermal index involving SST and surface layer thickness, could be examined using available hydrometric data. Correlations between sea survivorship and food supply, especially food supply in the warm surface layer, would be more difficult to calculate because abundance of many prey species taken by salmon is poorly known. It must be emphasized that correlations prove or disprove nothing. Significant correlations (including the one noted above between seal numbers and salmon pre-fishery abundance) can be spurious, and lack of correlation can be due to excessive noise or insufficient sample sizes. Also, if salmon respond to changing water temperatures by shifting their distribution latitudinally to maintain themselves in thermally preferred habitat, the predicted correlations will not occur.

An experimental setting, either a large land-based tank or a sea-cage, could be used to directly test elements of temperature influenced susceptibility to predation. Experiments could include measuring the degree of foraging intensity under various regimes of temperature and food supply, measuring the effect of water temperature on swimming performance, and measuring the effects of foraging intensity and temperature on risk of capture by endothermic predators. Cairns (2001) gives further details on these methodologies, and also proposed a number of other approaches to investigate relations between salmon and their bird and seal predators. These include use of seal-induced scars on returning salmon to infer attack patterns and rate trends, investigation of diets of gannets, and intensive studies in estuaries where there is a greater chance that interactions between salmon and their predators can be measured and documented. The examination of the predatory behaviour of free-ranging seals through use of multiple instrument packages, including head-mounted video cameras, also has great promise in clarifying how endothermic predators interact with their prey (Davis et al. 1999).

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Table 1. Means, standard deviations (S.D.), and coefficients of variation (CV) in size at return and annual sea survivals of Atlantic salmon in eastern Canada.

Feature	**Location**	**Dates**	**Mean**	**S.D.**	**CV (%)**	**N**	**Mean of within-year CVs (%)**
Size of returning maiden salmon							
Fork length (cm) 1SW	Miramichi	1971-1999	53.6	2.0	3.7	29	5.6
Fork length (cm) 2SW	Miramichi	1971-1999	73.8	1.6	2.2	29	4.5
Weight (g) 1SW	Miramichi	1971-1991	1578	79	5	21	16.9
Weight (g) 2SW	Miramichi	1971-1991	4468	225	5	21	15.7
Survival between smolt exit and river return (%)[2]	Bec-Scie	1988-1995	1.4	0.3	20.6	8	
	de la Trinité	1984-1997	1.7	0.9	55.5	14	
	Saint-Jean	1989-1996	0.4	0.1	24.3	8	
	Catamaran	1990-1997	9.7	3.2	33.4	8	
	Highlands	1993-1997	1.9	0.8	40.7	5	
	Campbellton	1993-1997	6.6	2.3	34.4	5	
	Western Arm Brook	1977-1997	4.8	2.8	58.3	21	
	Northeast Trepassey	1986-1997	5.5	2.2	39.5	12	
	Rocky	1990-1997	3.3	0.7	22.3	8	
	Conne	1987-1997	5.3	2.4	45.8	11	

[1] Data from Moore et al. (1995) and G. Chaput (unpubl. data)

[2] Data from compilation by Cairns and Reddin (2000)

Table 2. Responses to environmental changes by marine-phase Atlantic salmon, and their consequences. + means increasing, - means decreasing, 0 means staying the same.

Environmental change		Consequence in the absence of behavioural response		Behavioural response to environmental change		Consequence in the presence of behavioural response	
SST	-	Growth	-	Foraging activity	+	Growth	0
		Mortality	+	Diving below thermocline	+	Mortality	+
Thickness of warm surface layer	-	Growth	-	Foraging activity	+	Growth	0
		Mortality	+	Diving below thermocline	+	Mortality	+
Food supply	-	Growth	-	Foraging activity	+	Growth	0
		Mortality	+	Diving below thermocline	+	Mortality	+
Food supply with warm surface layer	-	Growth	-	Foraging activity	+	Growth	0
		Mortality	+	Diving below thermocline	+	Mortality	+
Endothermic predator populations	+	Growth	0	Foraging activity	0	Growth	0
		Mortality	+	Diving below thermocline	0	Mortality	+

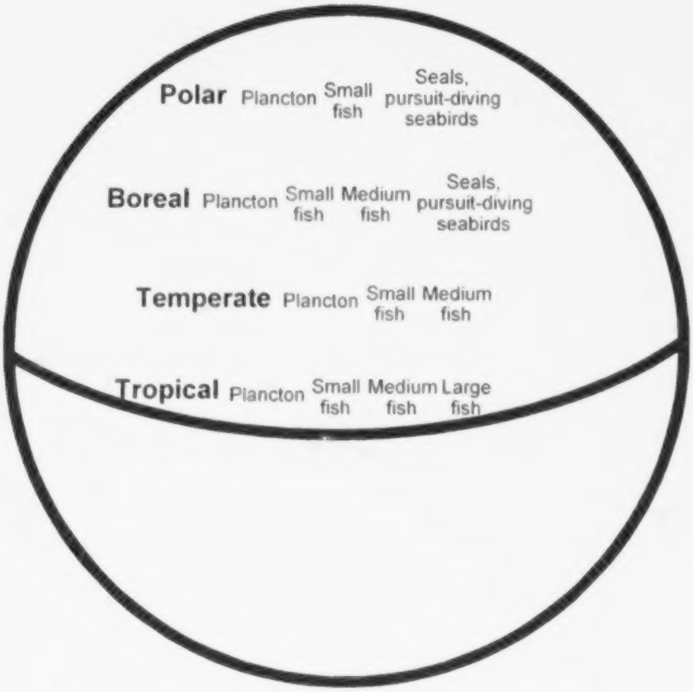

Polar
Plancton
Small fish
Seals, pursuit-diving seabirds
Boreal
Plancton
Small fish
Medium fish
Seals, pursuit-diving seabirds
Temperate
Plancton
Small fish
Medium fish
Tropical
Plancton
Small fish
Medium fish
Large fish

Figure 1. Simplified food chain in Polar, Boreal, Temperate and Tropical latitudes.

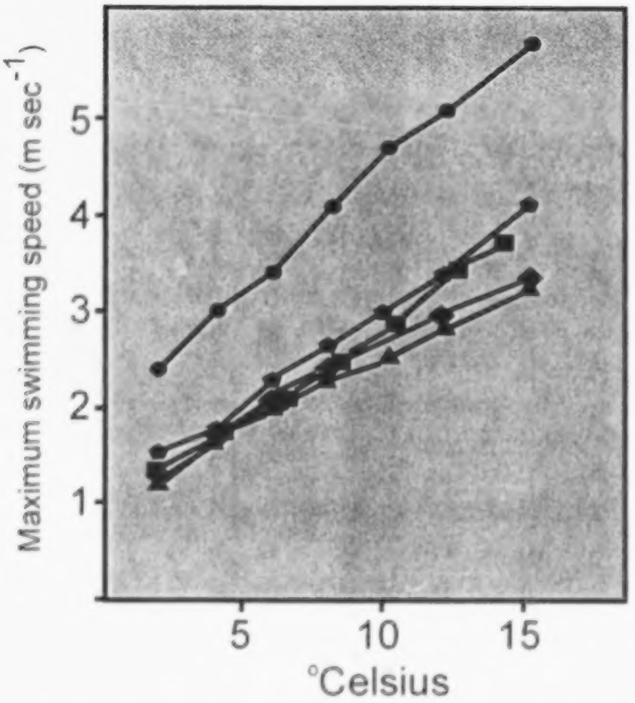


Figure 2. Maximum swimming speeds relative to water temperature of five fish species (from Wardle 1980).

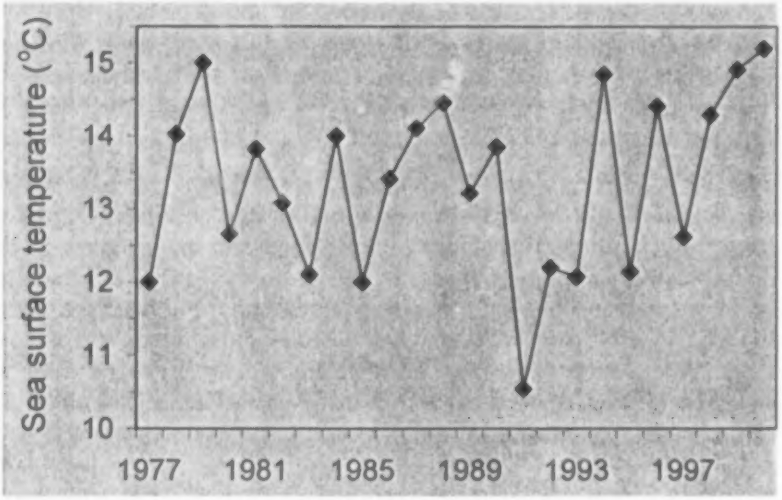
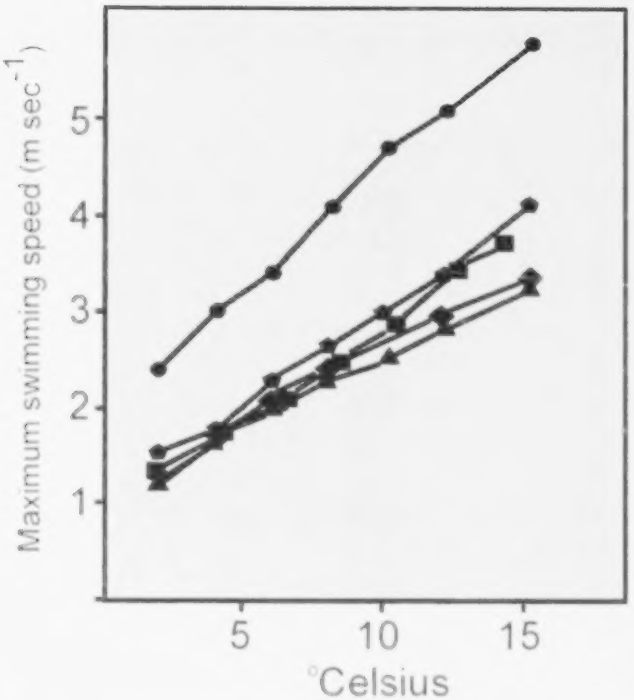


Figure 3. Mean August sea surface temperatures at Station 27, east of St. John's (Newfoundland), 1977 to 2000. In the three years where August records were unavailable (1978, 1981, 1982), August temperatures were estimated by regression based on July and September temperatures. Data from http://www.meds-sdmm.dfo-mpo.gc.ca/alphapro/zmp/climate/OffshoreHydro/Station27.shtml.



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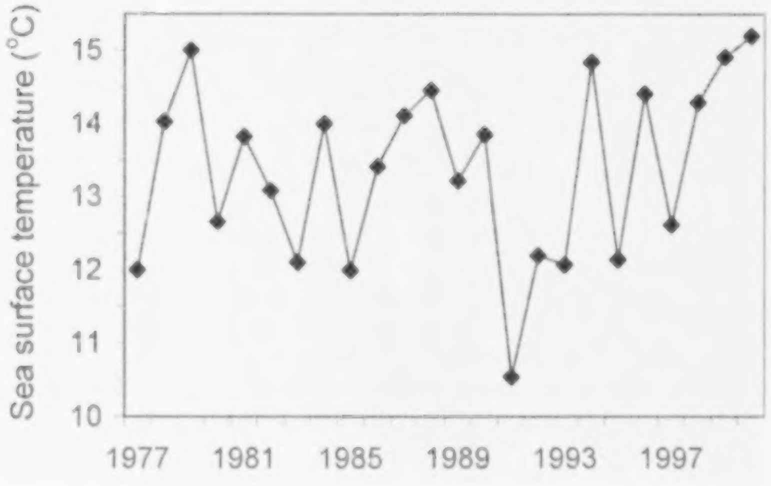

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12

FEEDING, FASTING, AND WEIGHT-BASED ESTIMATION OF NATURAL MORTALITY IN MARINE-PHASE ATLANTIC SALMON (*Salmo salar* L.)

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INTRODUCTION

Mortality can be more readily measured in Atlantic salmon (*Salmo salar* L.) than in virtually any other marine fish, because outgoing smolts and returning adults can be directly counted as they pass through river mouths. In the absence of fisheries or other anthropogenic impacts, natural mortality is simply the number of returning adults as a proportion of exiting smolts.

However, it is much more difficult to determine how natural mortality is distributed in time during the salmon's period at sea. There is a need to clarify the nature and temporal pattern of marine-phase mortality because of recent marked declines in estimated pre-fishery abundance (PFA) of Atlantic salmon of both European and North American origin (ICES 2000). Reliable estimates of M are also required as inputs to run-reconstruction models that convert river returns into PFA estimates. Models have until recently assumed that mortality is 1% per month after the first year at sea (ICES 2000). If actual mortality exceeds this figure, then the salmon decline indicated by models will be overstated (Meerburg et al. 2001).

A variety of methods are available for the estimation of M during the salmon's life at sea. These can be categorized according to their temporal specificity. Several methods can estimate total marine-phase M for fish with particular maturity schedules. These methods can give separate estimates of M for 1SW, 2SW fish etc., but do not indicate how M varies with time within the marine phase. Methods in this category include calculation of M required to maintain population stability given measured egg-to-smolt survival rates (Chaput 2003), and the estimation of M from longevity (Hoenig 1983), from Beverton and Holt life history invariants (Jensen 1996), from asymptotic weights (Ursin 1967) from growth parameters (Pauly 1980), and from mean gonadosomatic index (Gunderson 1997) (see reviews by McGurk 1999 and Chaput 2003).

Ricker (1976) reviewed a variety of methods that involve comparison of demographic characteristics of salmon with varying maturity schedules or sex ratios. Murphy's method (Ricker 1976), which is based on variation in maturity schedules between males and females, can be used to estimate M in each of the two sea years of a 2SW salmon (Jonasson et al. 1994, Chaput et al. 2003). Ocean tagging (Ricker 1976) can be used to determine mortality between tagging date and river return in populations in which fish return from the tagging site in the current year and at least one subsequent year.

An ample literature (Ricker 1976; McGurk 1986, 1996, 1999; Anderson 1988; Lorenzen 1996; Sogard 1997) reports a strong negative relation between M and body weight (W) in fishes. Thus models which relate M to W can be used to estimate M for any desired time period, provided that the curve of weight growth is known. M-W formulations assume that factors influencing mortality vary smoothly with weight. However, some animals undergo seasonal periods of inactivity or fasting, during which their vulnerability to mortality may be different than during regular active periods. Application of M-W models to the estimation of natural mortality must identify any periods when mortality is likely to differ from the norm, and make special provisions for them.

This paper examines the use of M-W relations for the estimation of M in marine-phase Atlantic salmon. Specifically, I a) plot growth curves for Atlantic salmon, and examine evidence for fasting by late-run fish in the summer prior to river return, b) calculate time-specific marine mortality by using the literature exponents of allometric equations, and adjusting the constant term until sea survival matches measured or arbitrarily-chosen plausible values, and c) review options for estimating M during the putative pre-return fasting period of late-run fish.

Weight-based approaches to estimating M have been previously applied to Atlantic salmon by Doubleday et al. (1979) and Cairns and Reddin (2000), and to Pacific salmon by Mathews and Buckley (1976), Ricker (1976), Furnell and Brett (1986), and McGurk (1996, 1999).

PERTINENT FEATURES OF ATLANTIC SALMON LIFE HISTORY

Atlantic salmon typically return to natal rivers after one (1SW) or two (2SW) sea winters, but many further variations occur, including multiple returns in either consecutive or alternate years. Salmon may return to rivers in spring, summer, or fall. During their period in rivers they eat little or not at all. Spawning occurs in fall.

There is a large literature on the life history of Atlantic salmon, which emphasizes the fitness consequences of sex ratio and maturity schedule variation (e.g. Mangel 1994; Hutchings and Jones 1998). However, some remarkable and puzzling attributes of marine-phase salmon seem to have escaped the attention of primary literature. These features are reviewed below.

Salmon growth and mortality rates

Salmon have exceptionally high growth rates while at sea (Fig. 1). Salmon weight increases approximately 75-fold between smolt exodus and return as 1SW adults, and 213-fold between smolt exodus and return as 2SW adults (Cairns 2001). Herring and mackerel occupy the same pelagic habitat in the Northwest Atlantic as salmon. Between the ages of 2 and 4, these fish are intermediate in size between exiting salmon smolts and returning adults (Fig. 1). During this period herring and mackerel weights increase by about 20-75% annually (Scott and Scott 1988). Hence growth rate of salmon is two or more orders of magnitude higher than those of their neighbours in the same habitat.

Because mortality risk decreases and reproductive potential increases with size, it is broadly desirable for fish to rapidly attain large weights (Sogard 1997). Anholt and Werner (1995) demonstrated in a laboratory setting that when tadpoles foraged actively, their growth rate increased, but their exposure to dragonfly predation also rose. These authors argued that growth-mortality trade-offs are a widespread phenomenon in nature. Grand (1999) used dynamic programming to examine how growth-mortality trade-offs influence time of smoltification in juvenile coho salmon. Trade-offs between growth and mortality have also been examined in salt marsh *Fundulus* (Halpin 2000), Muller's pearlsides (Giske and Aksnes 1992, Rosland and Giske 1994), juvenile coho salmon (Martell and Dill 1993), and fathead minnows (Abrahams and Pratt 2000).

If a growth-mortality trade-off operates in the marine life of Atlantic salmon, then salmon should pay for their high growth rate with a high mortality cost. Cairns and Reddin (2000) reviewed sea survivorship of salmon returning to eastern Canadian rivers between 1978 and 1998, and found survivorships ranging from 1.6% to 8.8%, with a mean of 3.7%. Based on Lorenzen's (1996) formula for ocean fishes, mackerel, herring, and cod of ages 3 and 4 have survivorships of 50%-60% (Fig. 2). Anthropogenic effects on sea survivorships of Northwest Atlantic salmon are uncertain, and true natural survivals might be higher that those tabulated by Cairns and Reddin (2000). Nevertheless it appears that salmon generally have much higher marine mortality rates than other fish that use the same habitat, at least in the northwest Atlantic.

Anholt and Werner (1995) showed that poor feeding conditions led to increased foraging activity in tadpoles, which in turn led to higher tadpole mortality from predation. A similar mechanism could operate in Atlantic salmon. Atlantic salmon returning to the Miramichi River show relatively little interannual variation in mean length and weight (Fig. 3) (a size increase in the early 1980s can be explained by the cessation of the commercial fishery which selected for larger sizes; Moore et al. 1995). In the 1990s, lengths of salmon returning to the Miramichi increased slightly, at a time when there was a general decline in sea survivals of North American Atlantic salmon. The relative stability of returnee sizes suggests that salmon aim to attain specific target sizes at return. To attain these sizes, they must adjust feeding intensity, or use of the surface layer where warmer water enhances growth, or both. These behaviours may increase predation risk because increased activity and use of surface layers will make salmon more visible and conspicuous to predators.

If salmon size at return, within sea-age categories, is relatively fixed, correlations between mortality and total marine growth should not be expected. However, there might be correlations between marine mortality and growth at shorter time periods. Crozier and Kennedy (1999) found no significant correlations between post-smolt growth and marine survival. Friedland et al. (1993) found a significant positive correlation between survival and circuli spacings, but only for the winter of sea age 0.

The relation between salmon behaviour at sea and mortality risk is presently unclear. However, recent work with temperature loggers fitted to free-ranging salmon may offer some clues. Loggers attached to Atlantic salmon and four species of Pacific salmon have indicated that fish spend much time near the surface, but also undergo rapid excursions up and down in the water column (Sturlaugsson 1995; Reddin et al. 1999, Walker et al. 2000). Such excursions occur in both day and night. Research fishing has shown that post-smolt salmon commonly swim near the ocean surface (Dutil and Coutu 1988). Post-smolts near the surface are vulnerable to the northern gannet, a large plunge-diving seabird (Montevecchi et al. 2002.). If vulnerability to other predators is also highest near the surface, then their behaviour with respect to vertical position may be an important factor in determining mortality risk.

Fasting in the summer prior to spawning

Long periods of hibernation, aestivation, and other forms of inactivity occur in many vertebrate animals. However, these periods of torpor normally coincide with seasonal food scarcity, or periods when temperatures are unsuitable for activity. Extended fasting may also occur in animals that are breeding (e.g. seals) or incubating eggs (e.g. ducks). Early-run salmon spend many months fasting in rivers, while they could be at sea increasing body size and gamete production. I am not aware of any vertebrates other than salmonids which fast for many months during the normal active season, in the absence of reproductive or physiological priorities which would prevent them from feeding.

In some rivers, it is conceivable that salmon enter early to take advantage of high discharges that will assist them in overcoming obstacles to upstream migration. However, early runs are also common in rivers such as the Miramichi that lack natural obstacles (although beaver dams might be more easily traversed in spring than later in the year). Salmon are competitive on the spawning grounds, and early arrival there could be an advantage in acquiring and holding spawning sites or mates. However, early-run salmon spend the summer in pools, and do not travel to spawning riffles until fall.

Large fish generally enjoy higher survivorship than small ones (Sogard 1997). If salmon commonly forego feeding for long periods during the normal growing season, then there must be a cost to doing so, and this cost must exceed the benefits conferred by summer feeding. The costs and advantages of fasting vs. feeding in the summer prior to spawning can be explored by modeling reproductive output as functions of growth rate, fecundity, and mortality for feeding and fasting populations. This analysis will be conducted after growth and mortality rates of Atlantic salmon are reviewed.

GROWTH

The nature of marine growth in Atlantic salmon

Growth of animals is commonly modelled by curves that are fitted to mean sizes at age for periods in which animals can be captured and measured. Cairns and Reddin (2000) took this approach to model growth of length and weight of marine-phase Atlantic salmon using logistic curves which tracked size increases during the growing season, and size stability during winter quiescence (Fig. 4). However, such composite curves may not reflect the actual growth of individual animals, because size-selective mortality may bias samples, and because typical animals may follow different growth trajectories than the composite mean.

Returning adult salmon enter the Miramichi River between May and October. Figs. 5 and 6 show length and weight records from research traps near the river mouth for 1986-1999 (length), and 1986-1991 (weight) (data from G. Chaput, DFO). Mean lengths of returning fish showed slight seasonal increases (Fig. 5). Mean weights of returning 1SW salmon were nearly stable, but mean weights of returning 2SW salmon declined slightly with season (Fig. 6).

If late-run salmon follow the composite growth curves presented in Fig. 4, they should be much longer and heavier upon river entry than early-run salmon. Two growth patterns could explain the similarity in size of early- and late-run fish. First, late-run fish could have a slower overall growth trajectory. Such fish, termed pre-return eaters (PRE), would be smaller in spring than early-run fish, but would continue to grow during the pre-return summer so that they attain similar size to early-returnees by the time they enter rivers late in the season. Second, late-run fish could grow in similar fashion to early returnees up to the time that early returnees enter rivers. Such fish, termed pre-return fasters (PRF), would stop eating in early summer, but remain at sea. Because they do not eat during the pre-return summer, their return weights would be similar to those of early returnees.

Fasting and movements in the pre-return summer

Blair (1965) sampled 919 salmon stomachs from the Bay of Islands, Newfoundland, between 1 June and 15 Aug 1942. Percent of stomachs containing food progressively decreased from 45.1 in 1-15 June to 0 in 1-15 August. Lear (1972) examined the contents of 2,350 salmon stomachs taken from coastal and offshore areas of the Northwest Atlantic. Most offshore stomachs were full, but 74-100% of stomachs sampled in the Saint John and Miramichi estuaries and near Carleton, on the Bay of Chaleur coast of Quebec, in June and early July were empty. Based on this finding, Lear (1972) suggested that Atlantic salmon feed almost continuously at sea, but cease feeding as they approach the estuaries of their natal rivers. Hansen (1996) and Jacobsen and Hansen (2000) reported that feeding activity of European Atlantic salmon tends to shut down during the homeward migration prior to river entry in early summer. Sturlaugsson (2000) referred to an absence of feeding among salmon returning to Iceland in September, despite an abundance of potential prey along the migration route. However, some returning salmon do take prey (including outgoing smolts) prior to river entry (Sturlaugsson 2000). Salmon in Scotland are reported to cease or markedly reduce feeding in June or early July, both in the wild (Fraser 1987) and in aquaculture sea-cages (Kadri et al. 1997). Summer anorexia is associated with maturity cycles. Fish which will mature in the fall fast during the summer, but fish which will not mature until the following year continue to feed (Kadri et al. 1995, 1996).

These studies indicate that the fasting behaviour which fish exhibit in rivers begins before river entry. Sampling in June and early July presumably includes early-run fish which would enter rivers soon after sampling. However, the studies quoted above do not indicate the run-time affinity of the fish captured for stomach analysis, so it is not possible to know whether samples included late-run fish. Hence these reports do not tell us whether late-run salmon exhibit PRE or PRF behaviour.

Belding and Préfontaine (1938, 1939) conducted extensive tagging studies in the Gulf of St. Lawrence, using commercial drift-net fisheries as a source of salmon for tagging and also for recoveries. They found that fish tagged at Port-aux-Basques, Newfoundland, were taken in a commercial drift-net fishery in Miramichi Bay which peaked in late June. Scales sampled from the Miramichi Bay fishery indicated 92.9% maiden 2SW fish, with the remainder being 3SW or previous spawners. Twenty fish tagged in Miramichi Bay were later captured in the Miramichi River and Estuary. Eleven were captured early (within three weeks of release) and eight were captured late (8 to 15 weeks after capture). A single fish was taken on 4 August.

Belding and Kitson (1934) stated that in June and July only a small percentage of salmon in coastal waters are still feeding. Belding and Préfontaine (1938, 1939) reported finding little food in salmon in Miramichi Bay after mid-June. These authors gave no details of methods or results of stomach analysis, so the intensity of sampling during the summer is unknown. In June and early July 1970, Reddin (1984) tagged salmon from the Miramichi Bay drift-net fishery. The catches included a mix of 1SW, 2SW, and older salmon. Sixty-five tags were recovered in the Miramichi River and Estuary. Timing of these recaptures was not reported.

Belding and Préfontaine's (1939) report of the dearth of feeding after mid-June, and the occurrence of fish tagged in early summer in Miramichi Bay in the fall run of the Miramichi River, is consistent with the PRF model of behaviour for 2SW fish. However, this evidence does not preclude the possibility that salmon also exhibit PRE behaviour, because some late-run fish might travel directly from offshore feeding grounds to the river, without an extended period of loitering off the river mouth. Belding and Préfontaine (1939) stated that 1SW fish were not caught in the Miramichi Bay drift-net fishery, and were taken commercially only in the river. Commercial nets described by these authors had mesh sizes of 16.5 cm, but by 1970, commercial mesh sizes in Miramichi Bay had decreased to 13.4-14.0 cm (Reddin 1984). Hence the lack of 1SW fish in Miramichi Bay drift-net catches in the 1930s was likely due, at least in part, to gear selectivity.

Scale data

Scales can also be used to infer patterns of marine growth of salmon (Friedland and Reddin 2000). Circuli counts and intercirculi spacings from 1SW and 2SW salmon entering the Margaree River are available (data and interpretations supplied by G. Chaput). Numbers of marine-zone circuli in scales sampled from 1SW and 2SW salmon returning to the Margaree increased from late June to through July, but thereafter circuli numbers were stable within each sea-age class (Fig. 7). This suggests that growth ceases after July. Intercirculi distances in scales sampled from spring, summer, and fall returnees on the Margaree showed similar patterns, which suggest similar growth rates among the groups (Fig. 8). Intercirculi distances of 1SW and 2SW maiden salmon showed generally parallel trends (Fig. 9). However, 1SW returnees showed spacings that were somewhat greater than those of 2SW fish during an initial growth period, and spacings that were much narrower than 2SW scales during the period prior to spawning by 1SW fish. This suggests that non-maturing fish grow rapidly during the 1SW summer, but maturing fish grow slowly or not at all. Since the majority of Margaree salmon are late-run, this period of non-growth would occur at sea.

The Margaree scale data support the PRF model of salmon behaviour for both 1SW and 2SW maturing fish. However, it must be noted that scale circuli counts and spacings show substantial intra-fish variation, and that circuli deposition patterns may not be an exact surrogate for growth rates.

Growth modelling

Growth models were created for both PRE and PRF behaviour patterns. Logistic curves were fitted to anchor points by eye and with the aid of Microsoft Excel Solver. This process was somewhat arbitrary because only one anchor point was used per year for sea ages 1SW and 2SW, and because no anchor points were available to fix overwintering sizes.

For both PRE and PRF growth models, logistic curves were fitted to three anchor points in the post-smolt year (Fig. 4, Figs. 10-15). The first anchor point was taken from sizes of exiting smolts captured in traps in the Miramichi River in 1998-2000 (Chaput et al. 2002). Fork length was 12.71 cm (SD=1.27, N=719) and weight was 21.35 g (SD=7.88, N=720). Date of river exit was taken as 23 May, which is the mean date of capture in the smolt traps. The two subsequent anchor points were from post-smolts recovered in a Newfoundland gannet colony in August (Montevecchi et al. 2002), and post-smolts captured in research cruises in the Labrador Sea in fall (Cairns and Reddin 2000).

In the 1SW year, modelled logistic growth rates split into three curves (Figs. 10 and 13). The first was fitted to lengths and weights of salmon returning on 1 July of sea age 1SW and 2SW. Sizes at these dates were calculated by the regression equations of length or weight vs. date for 1992-1999 (length, Fig. 5) and 1986-1991 (weight, Fig. 6). For middle- and late-run fish exhibiting PRE behaviour, curves were fitted to regressed size estimates for 15 August and 1 October in sea ages 1SW and 2SW (Figs. 10 and 13).

It was assumed that growth of PRF fish followed the trajectory plotted for PRE fish until the growth curve intersected with the regression lines for length and weight (Figs. 5-6). Thereafter, length and weight followed the lines predicted by these regression equations (Figs. 11-12 and 14-15). These curves showed sharp downward deflections in length growth for 1SW and 2SW fish and for weight growth of 1SW fish. In the case of 2SW fish, modelled weight decreased after June.

MORTALITY

Modelling approaches

Mortality-weight models have the form $M = M_u W^b$, where M_u is a constant, W is body weight, and b is the allometric exponent (notation is from Lorenzen 1996). There are two main approaches to estimating M_u and b. First, coefficients can be estimated from ecological theory. In an unexploited population at equilibrium, M equals the intrinsic rate of natural increase and the production: biomass ratio (Banse and Mosher 1980, Lorenzen 1996). Peterson and Wroblewski (1984) estimated that the exponent b has a value of -0.25, based on particle-size and predation theory. According to Dickie et al. (1987) and McGurk (1996), size dependency has a higher exponent within species or within closely related species than it does in the broad ecosystem. Based on size-dependency theory, McGurk (1996) suggested that the exponent b is -0.37 within individual species.

The second approach to estimating equation parameters is based on empirical relations between literature values for M and body size. McGurk (1986) found that M scaled to body weights of marine animals ranging in size from small pelagic invertebrates to whales with an exponent similar to the value theoretically derived by Peterson and Wroblewski (1984) (-0.25). Lorenzen (1996) surveyed available data for M and W of fish in lakes, rivers, and oceans, and calculated regression equations with exponents of -0.291, -0.289, and -0.305, respectively.

Use of M-W relations implies that, over the range of sizes for which M is estimated, major life history features are either relatively uniform through time or vary according to weight. If there are major discontinuities in life history features that may influence mortality, then the same M-W relation cannot be reliably applied before and after the discontinuity. The return of adult salmon from the sea to freshwater is one such discontinuity. Hence an M-W relation for the open sea could not be applied with confidence to the freshwater period. Serious bias in mortality estimates from M-W relations should not result if salmon which stop feeding as they approach the coast enter rivers soon after feeding cessation.. However, if late-return fish fast during the summer prior to river entry, then the normal M-W relation cannot be applied to this period.

Estimates of M

Mortality was modelled under a variety of assumptions with respect to sea age at return, return date, growth type, and mortality type. Post-smolts commonly encounter high levels of predation when they enter estuaries, and osmotic stress may heighten their susceptibility to capture (Larsson 1985, Hislop and Shelton 1993). To reflect this potential factor, mortality was modelled assuming mortalities of 0%, 20%, and 40% immediately upon river exit.

Tables 1-9 model mean monthly mortality rates at sea, under various scenarios. Figs. 16-17 plot instantaneous daily mortality curves for selected model scenarios. These plots show mortality as instantaneous daily mortality. A second Y axis gives percent monthly mortality. This axis gives a reasonable approximation of monthly mortality, but is not absolutely accurate because arithmetic mortality is not a linear function of instantaneous mortality.

Table 1 models mortality when mortality rates are a constant 1% during the period at sea. At this mortality rate, sea survival to 1 July of sea age 1 is 87.7%, 70.2%, and 52.6%, assuming mortality at river exit of 0%, 20%, and 40%. Table 1 also models mortality when sea survival to 1 July of sea age 1 is assumed to be 3.7% (the mean value of measured North American survivals, Cairns and Reddin 2000), and a range of other survivals (1%, 5%, 10%). Sea survival is assumed to be uniform. Under these circumstances monthly mortalities were 16.2-29.8% for 0% river exit mortality, and 12.8-27.0% for 40% river exit mortality.

Mortality was modelled using logistic curves for fish returning on 1 July, 15 August, and 1 October of sea age 2 (Table 2, Fig. 16), and Lorenzen's (1996) equation for the mortality of ocean fishes. Mortality trajectories differed little with respect to return date (Fig. 16). Survivorships to 1 July of sea age 1 were 52.4-52.6% for 0% river exit mortality, 42.0-42.1% for 20% river exit mortality, and 31.5-31.6% for 40% river exit mortality.

Table 3 models mortality of fish returning to rivers on 1 July of sea age 2. Mortality is estimated by an allometric weight function, with the exponent from Lorenzen's (1996) equation for ocean fishes (-0.305), and the constant adjusted to yield sea survivorships on 1 July of sea age 1 of 1, 3.7, 5, and 10%. Given 1SW sea survivals of 3.7%, monthly mortality rates just prior to river return were 11.5% for 0% river exit mortality, 10.7% for 20% exit mortality, and 9.8% for 40% exit mortality.

Sea survivals of salmon in the Northeast Atlantic are often higher than those of the Northwest Atlantic, and survivals greater than 20% are common in some areas (O Maoiléidigh et al. 2003). To reflect this broad range of survivorships, mortality was modeled according to the assumptions above, but with sea survivorships ranging from 1% to 40% (Table 4). When river exit mortality was assumed to be 20% and sea survivorship was 40%, monthly mortality just prior to return at sea age 2 was 2.5%.

In Table 5, mortality is modeled under the same terms as Table 3, except that the allometric exponent is taken from McGurk (1996) (-0.37). The use of the McGurk (1996) exponent produced slightly lower mortalities just before river return (9.7% at 0% exit mortality, 9.1% at 20% exit mortality, 8.3% at 40% exit mortality).

Tables 6 and 7 model mortalities using the Lorenzen (1996) exponent, the allometric constant adjusted to yield given sea survivorships, and return dates in sea age 2 of 15 August and 1 October, respectively. Growth rates were logistic, hence the fish behaved as PRE. Mortalities calculated under these assumptions were slightly lower than those based on the assumption that fish returned on 1 July (Table 3).

Table 8 and Fig. 17 present mortalities of fish showing logistic growth up to early summer of sea age 1, and thereafter growth set by date-weight regression equations. River exit mortality is assumed to be 20%. When mortality is allometric, it declines smoothly with increasing weight until the beginning of July, when it stabilises due to the levelling out of weights. Under PRF behaviour, weight of late-run fish prior to river return is set by regression and fish are assumed to fast during this period. Mortality during this period was arbitrarily set at 1% per month. Under these assumptions, mortality, which had been about 10-20% per month in spring, dropped abruptly at the beginning of summer (Fig. 17).

When similar assumptions were modelled for fish returning on 15 August and 1 October of sea age 2, similar mortality patterns ensued (Table 9). When mortality was assumed to be allometric throughout, mortality increased slightly during the summer period when the regression equation indicated shrinking weights. When mortality was arbitrarily assumed to be 1% per month during PRF behaviour, mortality decreased sharply on 1 July.

Estimation of M for pre-return fasting periods

If the salmon's high marine mortality is related to its feeding behaviour, as argued above, then mortality should be much lower when the animal is not feeding. This means that normal M-W relations will not be valid during this period.

None of the various methods proposed for the estimation of M in salmon and other fish (see Introduction) appears to be applicable to PRF behaviour, primarily because they cannot estimate M for periods of less than a year.

Many rivers support both early and late runs within each maturity age. If the proportion of early and late fish is constant year after year, then in-river mortality of early-run fish should equal at-sea mortality of late-run fish exhibiting PRF behaviour. If mortality of one group is higher than the other, then the proportion of the total run contributed by that group should diminish. Hence in any river where early and late runs are at equilibrium, marine M of PRF fish can be estimated as the measured value of in-river mortality of early-run fish.

The method proposed above is subject to additional caveats. It assumes that the fasting period of early- and late-run fish is similar, and that reproductive fitness is not altered by run timing. In practical terms, determination of stability of early and late contributions to the total run may be complicated by variations in the seasonal patterns of river discharge, which may influence run timing.

The fact that early-run salmon refrain from eating for many months preceding spawning is a remarkable and puzzling feature of salmon life history. If further investigations confirm that late-run salmon also fast during the summer, the puzzle would be all the more peculiar. Tables 10-11 and Figs. 18-19 present a model which may shed insight into pre-spawning fasts of Atlantic salmon, and which, pending additional data, might be used to set bounds on levels of marine mortality which salmon commonly experience.

Consider a population of 1,000 female salmon that are fasting during the pre-spawning summer, either at sea or in the river. Mortality is arbitrarily set at 1% per month. Potential egg deposition from this population is the product of population, after discounting for mortality, and fecundity, which is a function of weight (Tables 10-11). Potential egg deposition is estimated at 2.5 million for 1SW fish and 4.5 million for 2SW fish.

Now consider an alternate population of 1,000 females that remain at sea during the pre-spawning summer, and feed actively. These fish increase in fecundity because they grow, but they are subject to substantial mortality, as estimated by allometric equations. The question is: what is the overall sea survival rate at which the potential egg deposition of the feeding population surpasses that of the fasting population? Under the modelled assumptions, the equivalency point is 10.57% sea survival for 1SW fish (Table 10, Fig. 18). For 2SW fish, the equivalency point is 1.9% survival to 1 July of the 1SW year (Table 11, Fig. 19). This means that, if sea survival of 1SW returnees is less than the equivalency point (10.57% under model assumptions), fish are better off fasting during the pre-spawning summer than actively feeding. Since many (or most, if PRF behaviour is common) salmon fast in the pre-spawning summer, then sea survival must be typically less than the equivalency point.

This modeling approach depends on knowledge of mortality during pre-spawning fasting. Actual equivalency points of feeding vs. fasting behaviour can only be estimated when reliable mortality rates during fasting are available.

DISCUSSION

This paper has shown that marine mortality in Northwest Atlantic salmon is high compared with estimates for other pelagic fishes that use the same region, and that this high mortality is a predictable consequence of the species' rapid growth rate.

The approach used in mortality modeling in this study was to assume real or plausible overall sea survivals, and then adjust values or equation parameters to achieve these survivals. Model outputs indicated the temporal distribution of total marine mortality. Run-reconstruction models have previously assumed 1% monthly mortality between spring of the 1SW year and river return. When 1% mortality was uniformly applied throughout the marine phase, sea survival to 1 July of sea age 1SW was unrealistically high (>50%) (Table 1). When plausible sea survivals were assumed, and mortality was assumed to be uniform, monthly mortalities were 15-35% (Table 1). Mortalities for 1SW and 2SW fish as modelled by allometric equations under various assumptions were in the range of 5-16% per month (Tables 3-7). These results suggest that, if mortality is dependent on body weight, then actual mortality between 1SW spring and river return is much higher than the 1% per month assumed by the run-reconstruction models.

If 1% per month is the true mortality in the periods modeled by run-reconstruction models, and mortality is an allometric function of weight, then the decline in mortality with increasing weight must be far steeper than that indicated by any of the published M-W relations.

Evidence assembled in this paper hints that late-run salmon may fast in the summer prior to river entry, but the evidence is far from conclusive. If late run fish do exhibit PRF behaviour, then allometric models that predict M from W cannot be applied to these periods. Hence the application of allometric mortality models to marine-phase salmon hinges on determination of whether or not late-run salmon show PRF behaviour. At a broader scale, the clarification of this question is a key precursor to understanding the life history of Atlantic salmon at sea.

The following methods may help determine the behaviour of late-run salmon in their pre-spawning summer:

a) Examination of recapture records from the 1970 drift-net tagging study (Reddin 1984) would reveal if some salmon that arrive in Miramichi Bay in early summer enter the Miramichi as fall-run fish.

b) Tagging and diet studies. Following the example of Reddin (1984), salmon could be sampled and tagged in Miramichi Bay, using nets of a range of mesh sizes that would capture all sizes of adult salmon. Sampling would continue from June through to fall. Representative samples would be taken to determine stomach fullness. Monitoring of assessment traps for tag recoveries would indicate whether late-run fish summered without feeding in Miramichi Bay.

c) Further analysis of scale circuli patterns would shed additional light on growth patterns prior to river return.

d) Anorexic behaviour in the spring prior to spawning is a powerfully pre-programmed behaviour in aquaculture salmon in Scotland (Kadri et al. 1997). These fish are presumably many generations removed from the selective pressures that produced such behaviour patterns. If there are strains of salmon of late-run origin that are held in captivity in research or aquaculture settings, the feeding appetite of these fish could be monitored in the summer prior to spawning. If these fish fast during this period, it would support the hypothesis that pre-spawning fasting occurs in both early and late returnees.

e) Doucett et al. (1999) showed that concentrations of lipids and other energy reserves decline, and isotopes of C and N become enriched, in specific organs within adult Atlantic salmon that have entered rivers. These changes were attributed to the energy requirements of upstream migration and to the progressive mobilization of nutrient reserves due to fasting. Comparisons of lipid and other concentrations and isotope enrichments of salmon sampled on feeding grounds, in early summer off natal river mouths, and from early and late returnees might indicate whether late returnees have been eating during the pre-return summer.

An additional area for research initiatives is the estimation of in-river mortality of returning adults. Energetic costs of this phase of a salmon's life have been calculated (Jonsson et al. 1997; Rand and Hinch 1998), but mortality rates appear to have drawn little attention. In-river mortality could presumably be estimated from marking and recapture data in rivers where salmon are trapped at river entry and also at upstream sites. Such estimates would provide a means of estimating at-sea mortality under PRF conditions. They would also serve as inputs for models which investigate the reasons that many salmon forego the opportunity to gain weight and increase gamete output during the summer before spawning.

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Table 1

Marine mortalities of Atlantic salmon, assuming uniform mortality with time

Model parameters[a]	Scenario set	1	2	3	4	4	4	4	5	5	5	5	6	6	6	6
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul
	Growth model	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Mortality type	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform
	Mortality at river exit (%)	0	20	40	0	0	0	0	20	20	20	20	40	40	40	40
	Allometric formula: M_u, d^{-1}	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Allometric formula [b]	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Mortality when wt. calc. by reg.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	0.00032	0.00032	0.00032	0.0114	0.0082	0.0074	0.0057	0.0108	0.0076	0.0069	0.0051	0.0101	0.0069	0.0062	0.0044
	Sea survivorship (%)															
	to 1 Jul, sea age 1	87.7	70.2	52.6	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	86.5	69.2	51.9	0.6	2.6	3.6	7.7	0.6	2.6	3.7	7.9	0.6	2.7	3.8	8.2
	to 1 Oct, sea age 1	85.1	68.1	51.1	0.4	1.7	2.5	5.9	0.4	1.8	2.7	6.2	0.4	2.0	2.8	6.6
	to 1 Jul, sea age 2	77.9	62.3	46.8	0.0	0.2	0.3	1.2	0.0	0.2	0.4	1.5	0.0	0.3	0.5	2.0
	to 15 Aug, sea age 2	77.9	62.3	46.7	0.0	0.2	0.3	1.2	0.0	0.2	0.4	1.5	0.0	0.3	0.5	2.0
	to 1 Oct, sea age 2	77.9	62.3	46.7	0.0	0.2	0.3	1.2	0.0	0.2	0.4	1.5	0.0	0.3	0.5	2.0
Mean instantaneous daily mortality	Sea age 0	0.00032	0.00032	0.00032	0.011	0.0082	0.0074	0.0057	0.0108	0.0076	0.0069	0.0051	0.0101	0.0069	0.0062	0.0044
	Sea age 1	0.00032	0.00032	0.00032	0.011	0.0082	0.0074	0.0057	0.0108	0.0076	0.0069	0.0051	0.0101	0.0069	0.0062	0.0044
	Sea age 2	0.00032	0.00032	0.00032	0.011	0.0082	0.0074	0.0057	0.0108	0.0076	0.0069	0.0051	0.0101	0.0069	0.0062	0.0044
Mean monthly mortality (%)	Sea age 0	1.00	1.00	1.00	29.77	22.35	20.54	16.20	28.56	21.01	19.16	14.75	26.96	19.25	17.36	12.85
	Sea age 1	1.00	1.00	1.00	29.77	22.35	20.54	16.20	28.56	21.01	19.16	14.75	26.96	19.25	17.36	12.85
	Sea age 2	1.00	1.00	1.00	29.77	22.35	20.54	16.20	28.56	21.01	19.16	14.75	26.96	19.25	17.36	12.85

[a] Abbreviations: NA - not applicable, reg. - regression.

Table 2

Marine mortalities of Atlantic salmon, assuming mortality as estimated by Lorenzen's (1996) formula for ocean fishes

Model parameters[a]	Scenario set	7	7	7	8	8	8	9	9	9
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	1 Jul	15 Aug	1 Oct	1 Jul	15 Aug	1 Oct	1 Jul	15 Aug	1 Oct
	Growth model	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic
	Mortality type	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.	Allo.,Lor.
	Mortality at river exit (%)	0	0	0	20	20	20	40	40	40
	Allometric formula: M_u d^{-1}	0.0101	0.0101	0.0101	0.0101	0.0101	0.0101	0.0101	0.0101	0.0101
	Allometric formula: ^{b}	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)									
	to 1 Jul, sea age 1	52.6	52.5	52.4	42.1	42.0	42.0	31.6	31.5	31.5
	to 15 Aug, sea age 1	50.3	49.9	49.9	40.2	40.0	39.9	30.2	30.0	29.9
	to 1 Oct, sea age 1	48.2	47.6	47.4	38.5	38.1	37.9	28.9	28.6	28.4
	to 1 Jul, sea age 2	38.3	37.0	36.4	30.6	29.6	29.1	23.0	22.2	21.9
	to 15 Aug, sea age 2	37.9	35.7	35.0	30.3	28.6	28.0	22.7	21.4	21.0
	to 1 Oct, sea age 2	37.9	35.7	33.7	30.3	28.5	27.0	22.7	21.4	20.2
Mean instantaneous daily mortality	Sea age 0	0.00211	0.00211	0.00211	0.00211	0.00211	0.00211	0.00211	0.00211	0.00211
	Sea age 1	0.00104	0.00109	0.00111	0.00104	0.00109	0.00111	0.00104	0.00109	0.00111
	Sea age 2	0.00082	0.00088	0.00090	0.00082	0.00088	0.00090	0.00082	0.00088	0.00090
Mean monthly mortality (%)	Sea age 0	6.28	6.28	6.28	6.28	6.28	6.28	6.28	6.28	6.28
	Sea age 1	3.16	3.32	3.39	3.16	3.32	3.39	3.16	3.32	3.39
	Sea age 2	2.50	2.69	2.75	2.50	2.69	2.75	2.50	2.69	2.75

[a] Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric, Lor. - Lorenzen's (1996) formula for ocean fishes

Table 3

Marine mortalities of Atlantic salmon, assuming river return on 1 July at sea age 2, logistic growth, and allometric mortality

Model parameters[a]	Scenario set	10	10	10	10	11	11	11	11	12	12	12	12
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul
	Growth model	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic
	Mortality type	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.
	Mortality at river exit (%)	0	0	0	0	20	20	20	20	40	40	40	40
	Allometric formula: M_o, d^{-1}	0.072	0.052	0.047	0.036	0.069	0.048	0.044	0.033	0.064	0.044	0.039	0.028
	Allometric formula: b	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)												
	to 1 Jul, sea age 1	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	0.7	2.9	4.0	8.5	0.7	3.0	4.1	8.6	0.7	3.0	4.2	8.8
	to 1 Oct, sea age 1	0.5	2.4	3.3	7.3	0.5	2.4	3.4	7.5	0.6	2.5	3.6	7.8
	to 1 Jul, sea age 2	0.1	0.7	1.1	3.2	0.1	0.8	1.3	3.6	0.1	0.9	1.5	4.1
	to 15 Aug, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	to 1 Oct, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mean instantaneous daily mortality	Sea age 0	0.0151	0.0108	0.0098	0.0076	0.0144	0.0101	0.0091	0.0068	0.0134	0.0091	0.0081	0.0059
	Sea age 1	0.0074	0.0053	0.0048	0.0037	0.0071	0.0050	0.0045	0.0034	0.0066	0.0045	0.0040	0.0029
	Sea age 2	0.0059	0.0042	0.0038	0.0029	0.0056	0.0039	0.0035	0.0027	0.0052	0.0036	0.0032	0.0023
Mean monthly mortality (%)	Sea age 0	36.18	27.76	25.64	20.46	34.83	26.20	24.03	18.73	33.04	24.12	21.88	16.40
	Sea age 1	20.54	15.18	13.90	10.87	19.65	14.23	12.94	9.87	18.49	12.99	11.68	8.57
	Sea age 2	16.64	12.22	11.17	8.70	15.90	11.44	10.38	7.89	14.94	10.43	9.35	6.84

[a] Abbreviations: NA - not applicable; reg. - regression; Allo. - allometric

Table 4

Marine mortalities of Atlantic salmon by month, assuming river return on 1 Jul at sea age 1. A broad range (1-40%) of sea survivals is modeled.

Model parameters[a]	Scenario set	13	13	13	13	14	14	14	14	15	15	15	15	16	16	16	16
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul
	Growth model	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic
	Mortality type	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo	Allo
	Mortality at river exit (%)	0	0	0	0	20	20	20	20	40	40	40	40	60	60	60	60
	Allometric formula M_r d^{-1}	0.072	0.036	0.025	0.014	0.069	0.033	0.022	0.011	0.064	0.028	0.017	0.006	0.058	0.022	0.011	NA
	Allometric formula ^{b}	-0.305	-0.205	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)																
	to 1 Jul. sea age 1	1.0	10.0	20.0	40.0	1.0	10.0	20.0	40.0	1.0	10.0	20.0	40.0	1.0	10.0	20.0	40.0
	to 15 Aug. sea age 1	0.7	8.5	17.9	37.5	0.7	8.6	18.1	38.1	0.7	8.8	18.5	38.9	0.8	9.1	19.0	40.0
	to 1 Oct. sea age 1	0.5	7.3	16.0	35.3	0.5	7.5	16.5	36.4	0.6	7.8	17.2	37.8	0.6	8.3	18.2	40.0
	to 1 Jul. sea age 2	0.1	3.2	9.0	25.4	0.1	3.6	10.1	28.4	0.1	4.1	11.6	32.7	0.2	5.0	14.2	40.0
	to 15 Aug. sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	to 1 Oct. sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mean instantaneous daily mortalit	Sea age 0	0.0151	0.0076	0.0053	0.0030	0.0144	0.0068	0.0045	0.0023	0.0134	0.0059	0.0036	0.0013	0.0121	0.0045	0.0023	
	Sea age 1	0.0074	0.0037	0.0026	0.0015	0.0071	0.0034	0.0022	0.0011	0.0066	0.0029	0.0018	0.0007	0.0060	0.0022	0.0011	
	Sea age 2	0.0059	0.0029	0.0021	0.0012	0.0056	0.0027	0.0018	0.0009	0.0052	0.0023	0.0014	0.0005	0.0047	0.0018	0.0009	
Mean monthly mortality (%)	Sea age 0	36.18	20.48	14.89	8.82	34.83	18.73	12.99	6.76	33.03	16.40	10.47	4.02	30.42	12.99	6.76	
	Sea age 1	20.54	10.87	7.73	4.48	19.65	9.87	6.70	3.41	18.49	8.57	5.34	2.01	16.83	6.70	3.41	
	Sea age 2	16.64	8.70	6.16	3.56	15.90	7.89	5.33	2.70	14.94	6.84	4.25	1.59	13.57	5.33	2.70	

[a]Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric

Table 5

Marine mortalities of Atlantic salmon, assuming river return on 1 Jul at sea age 2, logistic growth using the exponent of McGurk's (1996) equation, and allometric mortality.

Model parameters[a]													
	Scenario set	17	17	17	17	18	18	18	18	19	19	19	19
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul	1 Jul
	Growth model	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic
	Mortality type	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.
	Mortality at river exit (%)	0	0	0	0	20	20	20	20	40	40	40	40
	Allometric formula: $M_u\ d^{-1}$	0.105	0.075	0.068	0.053	0.100	0.070	0.063	0.048	0.094	0.064	0.057	0.041
	Allometric formula: ^{b}	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370	-0.370
	Mortality when wt. calc. by reg	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)												
	to 1 Jul, sea age 1	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	0.7	3.0	4.1	8.7	0.8	3.1	4.2	8.8	0.8	3.1	4.3	8.3
	to 1 Oct, sea age 1	0.6	2.5	3.5	7.6	0.6	2.6	3.6	7.8	0.6	2.6	3.7	8.1
	to 1 Jul, sea age 2	0.1	0.9	1.4	3.7	0.2	1.0	1.5	4.1	0.2	1.1	1.7	4.7
	to 15 Aug, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	to 1 Oct, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mean instantaneous daily mortality	Sea age 0	0.0161	0.0115	0.0104	0.0080	0.0153	0.0107	0.0097	0.0073	0.0143	0.0097	0.0087	0.0062
	Sea age 1	0.0067	0.0048	0.0043	0.0033	0.0063	0.0044	0.0040	0.0030	0.0059	0.0040	0.0036	0.0026
	Sea age 2	0.0050	0.0036	0.0032	0.0025	0.0048	0.0033	0.0030	0.0023	0.0044	0.0030	0.0027	0.0019
Mean monthly mortality (%)	Sea age 0	37.29	28.82	26.67	21.40	35.94	27.24	25.03	19.60	34.14	25.13	22.83	17.20
	Sea age 1	18.60	13.71	12.54	9.79	17.79	12.85	11.67	8.89	16.73	11.72	10.52	7.71
	Sea age 2	14.34	10.49	9.58	7.45	13.69	9.81	8.90	6.75	12.85	8.94	8.01	5.84

[a] Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric

Table 6

Marine mortalities of Atlantic salmon, assuming river return on 15 August at sea age 2, logistic growth, and allometric mortality.

Model parameters[a]	Scenario set	20	20	20	20	21	21	21	21	22	22	22	22
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug
	Growth model	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic
	Mortality type	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.
	Mortality at river exit (%)	0	0	0	0	20	20	20	40	40	40	40	40
	Allometric formula: M_u d^{-1}	0.072	0.052	0.047	0.036	0.069	0.048	0.043	0.028	0.064	0.044	0.039	0.028
	Allometric formula: [b]	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)												
	to 1 Jul, sea age 1	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	0.7	2.9	4.0	8.4	0.7	2.9	4.0	8.7	0.7	3.0	4.1	8.7
	to 1 Oct, sea age 1	0.5	2.3	3.2	7.1	0.5	2.3	3.3	7.6	0.5	2.4	3.4	7.6
	to 1 Jul, sea age 2	0.1	0.6	1.0	2.9	0.1	0.7	1.1	3.8	0.1	0.8	1.3	3.8
	to 15 Aug, sea age 2	0.1	0.5	0.8	2.5	0.1	0.6	1.0	3.4	0.1	0.7	1.1	3.4
	to 1 Oct, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mean instantaneous daily mortality	Sea age 0	0.0150	0.0108	0.0098	0.0075	0.0143	0.0100	0.0091	0.0058	0.0134	0.0091	0.0081	0.0058
	Sea age 1	0.0078	0.0056	0.0051	0.0039	0.0074	0.0052	0.0047	0.0030	0.0069	0.0047	0.0042	0.0030
	Sea age 2	0.0063	0.0045	0.0041	0.0031	0.0060	0.0042	0.0038	0.0024	0.0056	0.0038	0.0034	0.0024
Mean monthly mortality (%)	Sea age 0	36.05	27.66	25.55	20.40	34.71	26.10	23.93	16.34	32.92	24.03	21.79	16.34
	Sea age 1	21.39	15.83	14.49	11.34	20.47	14.84	13.49	8.94	19.26	13.55	12.18	8.94
	Sea age 2	17.68	13.00	11.89	9.27	16.90	12.18	11.06	7.29	15.89	11.11	9.97	7.29

[a] Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric

Table 7

Marine mortalities of Atlantic salmon, assuming river return on 1 Oct at sea age 2, logistic growth, and allometric mortality

Model parameters[a]	Scenario set	23	23	23	23	24	24	24	24	25	25	25	25
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct
	Growth model	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic	Logistic
	Mortality type	Allo.	Allo.	Allo	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo.	Allo	Allo.
	Mortality at river exit (%)	0	0	0	0	20	20	20	20	40	40	40	40
	Allometric formula: M_u d^{-1}	0.072	0.052	0.047	0.036	0.069	0.048	0.043	0.033	0.064	0.044	0.039	0.028
	Allometric formula: ^{b}	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)												
	to 1 Jul, sea age 1	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	0.7	2.9	4.0	8.4	0.7	2.9	4.0	8.5	0.7	3.0	4.1	8.7
	to 1 Oct, sea age 1	0.5	2.2	3.1	7.0	0.5	2.3	3.2	7.2	0.5	2.4	3.4	7.6
	to 1 Jul, sea age 2	0.1	0.6	0.9	2.7	0.1	0.7	1.0	3.1	0.1	0.8	1.2	3.6
	to 15 Aug, sea age 2	0.1	0.5	0.8	2.4	0.1	0.5	0.9	2.7	0.1	0.6	1.1	3.3
	to 1 Oct, sea age 2	0.0	0.4	0.6	2.1	0.0	0.5	0.7	2.4	0.1	0.5	0.9	2.9
Mean instantaneous daily mortality	Sea age 0	0.0150	0.0108	0.0098	0.0075	0.0143	0.0100	0.0090	0.0068	0.0134	0.0091	0.0081	0.0058
	Sea age 1	0.0079	0.0057	0.0052	0.0040	0.0076	0.0053	0.0048	0.0036	0.0071	0.0048	0.0043	0.0031
	Sea age 2	0.0064	0.0046	0.0042	0.0032	0.0061	0.0043	0.0039	0.0029	0.0057	0.0039	0.0035	0.0025
Mean monthly mortality (%)	Sea age 0	36.05	27.66	25.54	20.40	34.70	26.10	23.93	18.65	32.92	24.03	21.79	16.33
	Sea age 1	21.81	16.15	14.79	11.58	20.88	15.15	13.77	10.52	19.65	13.83	12.44	9.13
	Sea age 2	18.06	13.29	12.15	9.48	17.26	12.45	11.30	8.60	16.23	11.35	10.19	7.46

[a] Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric

Table 8

Marine mortalities of Atlantic salmon by month, assuming river return at sea age 1. Growth is logistic up to 1 July of sea age 1, thereafter growth is by regression formula. Mortality is allometric, except after 1 July, sea age 1, in Scenarios 27 and 29, when mortality is assumed to be 1% per month under Pre-Return Fasting behaviour.

Model parameters[a]	Scenario set	26	26	26	26	27	27	27	27	28	28	28	28	29	29	29	29
	Sea age at return	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW	1SW
	Return date	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct
	Growth model	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.	Log./Reg.
	Mortality type	Allo.	Allo.	Allo.	Allo.	Allo./Uni.	Allo./Uni.	Allo./Uni.	Allo./Uni.	Allo.	Allo.	Allo.	Allo.	Allo./Uni.	Allo./Uni.	Allo./Uni.	Allo./Uni.
	Mortality at river exit (%)	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
	Allometric formula: M_0, d^{-1}	0.069	0.048	0.044	0.033	0.069	0.048	0.044	0.033	0.069	0.048	0.044	0.033	0.069	0.048	0.044	0.033
	Allometric formula: b	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg.	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)																
	to 1 Jul, sea age 1	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	0.7	2.9	4.1	8.6	1.0	3.6	4.9	9.8	0.7	2.9	4.1	8.6	1.0	3.6	4.9	9.8
	to 1 Oct, sea age 1	NA	NA	NA	NA	NA	NA	NA	NA	0.5	2.3	3.3	7.3	1.0	3.6	4.8	9.7
	to 1 Jul, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	to 15 Aug, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	to 1 Oct, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mean instantaneous daily mortality	Sea age 0	0.0144	0.0101	0.0091	0.0068	0.0144	0.0101	0.0091	0.0068	0.0144	0.0101	0.0091	0.0068	0.0144	0.0101	0.0091	0.0068
	Sea age 1	0.0077	0.0054	0.0049	0.0037	0.0060	0.0043	0.0039	0.0029	0.0076	0.0053	0.0048	0.0036	0.0049	0.0035	0.0031	0.0024
Mean monthly mortality (%)	Sea age 0	34.83	26.20	24.03	18.73	34.83	26.20	24.03	18.73	34.83	26.20	24.03	18.73	34.83	26.20	24.03	18.73
	Sea age 1	21.32	15.48	14.08	10.76	16.66	12.17	11.09	8.54	21.02	15.26	13.87	10.60	13.53	9.94	9.07	7.03

[a] Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric, Uni. - uniform

Table 9

Marine mortalities of Atlantic salmon, assuming river return at sea age 2. Growth is logistic up to 1 July of sea age 2, thereafter growth is by regression formula. Mortality is allometric, except after 1 July, sea age 2, in Scenarios 31 and 33, when mortality is assumed to be 1% per month under Pre-Return Fasting behaviour.

Model parameters[a]	Scenario set	30	30	30	30	31	31	31	31	32	32	32	32	33	33	33	33
	Sea age at return	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW	2SW
	Return date	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	15 Aug	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct	1 Oct
	Growth model	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg	Log /Reg
	Mortality type	Allometric	Allometric	Allometric	Allometric	Allo /Uni	Allo /Uni	Allo /Uni	Allo /Uni	Allometric	Allometric	Allometric	Allometric	Allo /Uni	Allo /Uni	Allo /Uni	Allo /Uni
	Mortality at river exit (%)	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
	Allometric formula: $M_u\ d^{-1}$	0.069	0.048	0.044	0.033	0.069	0.048	0.044	0.033	0.069	0.048	0.044	0.033	0.069	0.048	0.044	0.033
	Allometric formula: ^{b}	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305	-0.305
	Mortality when wt. calc. by reg.	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003	0.0003
	Uniform mortality rate	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sea survivorship (%)																
	to 1 Jul, sea age 1	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0	1.0	3.7	5.0	10.0
	to 15 Aug, sea age 1	0.7	3.0	4.1	8.6	0.7	3.0	4.1	8.6	0.7	3.0	4.1	8.6	0.7	3.0	4.1	8.6
	to 1 Oct, sea age 1	0.5	2.4	3.4	7.5	0.5	2.4	3.4	7.5	0.5	2.4	3.4	7.5	0.5	2.4	3.4	7.5
	to 1 Jul, sea age 2	0.1	0.8	1.3	3.6	0.1	0.8	1.3	3.6	0.1	0.8	1.3	3.6	0.1	0.8	1.3	3.6
	to 15 Aug, sea age 2	0.1	0.7	1.1	3.2	0.1	0.8	1.2	3.5	0.1	0.7	1.1	3.2	0.1	0.8	1.2	3.5
	to 1 Oct, sea age 2	NA	NA	NA	NA	NA	NA	NA	NA	0.1	0.6	0.9	2.8	0.1	0.8	1.2	3.5
Mean instantaneous daily mortality	Sea age 0	0.0144	0.0101	0.0091	0.0068	0.0144	0.0101	0.0091	0.0068	0.0144	0.0101	0.0091	0.0068	0.0144	0.0101	0.0091	0.0068
	Sea age 1	0.0071	0.0050	0.0045	0.0034	0.0071	0.0050	0.0045	0.0034	0.0071	0.0050	0.0045	0.0034	0.0071	0.0050	0.0045	0.0034
	Sea age 2	0.0056	0.0039	0.0035	0.0026	0.0043	0.0031	0.0028	0.0021	0.0055	0.0039	0.0035	0.0026	0.0035	0.0025	0.0023	0.0017
Mean monthly mortality (%)	Sea age 0	34.83	26.20	24.03	18.73	34.83	26.20	24.03	18.73	34.83	26.20	24.03	18.73	34.83	26.20	24.03	18.73
	Sea age 1	19.65	14.23	12.94	9.87	19.65	14.23	12.94	9.87	19.65	14.23	12.94	9.87	19.65	14.23	12.94	9.87
	Sea age 2	15.81	11.37	10.32	7.84	12.35	8.96	8.15	6.25	15.72	11.30	10.25	7.79	10.08	7.37	6.72	5.20

[a] Abbreviations: NA - not applicable, reg. - regression, Allo. - allometric, Uni. - uniform

Table 10

Fecundity, mortality, cohort size, and potential egg deposition of maiden 1SW Atlantic salmon returning to the Miramichi River at various times. Fecundity (2.035 eggs g^{-1}) is from Randall 1989. Weights and mortalities for salmon entering rivers after 1 July are from Scenario 23, Table 7 (logistic growth, return at 2SW on 1 Oct, 20% mortality upon river exit, allometric mortality using Lorenzen's (1996) b (-3.05), with Mu d^{-1} adjusted to yield given sea survivals).

Date	Salmon fast after 1 Jul					
	Wt. (g)	Fe-cund-ity	Mortality 1% $month^{-1}$			
			Instant-aneous daily mortality	Mon-thly mort. (%)	Cohort size	Potential egg deposition
Mortality eqn.: M_u d^{-1}			NA			
Mortality eqn.: b			NA			
1 Jul	1,278	2,600	0.0003	1.0	1,000	2,600,290
15 Jul	1,278	2,600	0.0003	1.0	995	2,588,514
1 Aug	1,278	2,600	0.0003	1.0	990	2,574,287
15 Aug	1,278	2,600	0.0003	1.0	986	2,562,629
1 Sep	1,278	2,600	0.0003	1.0	980	2,548,544
15 Sep	1,278	2,600	0.0003	1.0	976	2,537,003
1 Oct	1,278	2,600	0.0003	1.0	971	2,523,876

Date	Salmon remain at sea and feed after 1 Jul																					
	Wt (g)	Fe-cund-ity	Sea survival 1%				Sea survival 3.7%				Sea survival 5%				Sea survival 10%				Sea survival 10.57%			
			Instant-aneous daily mortality	Mon-thly mort. (%)	Cohort size	Potential egg deposition	Instant-aneous daily mortality	Mon-thly mort. (%)	Cohort size	Potential egg deposition	Instant-aneous daily mortality	Mon-thly mort. (%)	Cohort size	Potential egg deposition	Instant-aneous daily mortality	Mon-thly mort. (%)	Cohort size	Potential egg deposition	Instant-aneous daily mortality	Mon-thly mort. (%)	Cohort size	Potential egg deposition
Mortality eqn.: M_u d^{-1}			0.06865				0.04815				0.04343				0.02807				0.03170			
Mortality eqn.: b			-0.305				-0.305				-0.305				-0.305				-0.305			
1 Jul	1,278	2,600	0.0077	21.4	1,000	2,600,290	0.0054	15.5	1,000	2,600,290	0.0049	14.1	1,000	2,600,290	0.0037	10.8	1,000	2,600,290	0.0036	10.5	1,000	2,600,290
15 Jul	1,320	2,686	0.0077	21.2	898	2,411,191	0.0054	15.4	927	2,490,194	0.0049	14.0	934	2,508,739	0.0036	10.7	950	2,551,960	0.0035	10.4	951	2,555,473
1 Aug	1,382	2,812	0.0076	20.9	789	2,217,762	0.0053	15.2	847	2,380,774	0.0048	13.8	860	2,419,955	0.0036	10.5	893	2,512,623	0.0035	10.3	896	2,520,239
15 Aug	1,443	2,936	0.0075	20.7	710	2,083,624	0.0052	15.0	786	2,308,197	0.0047	13.6	805	2,363,216	0.0035	10.4	850	2,494,915	0.0034	10.1	854	2,505,836
1 Sep	1,527	3,108	0.0073	20.3	626	1,945,145	0.0051	14.7	720	2,237,335	0.0046	13.4	743	2,310,568	0.0035	10.2	801	2,488,403	0.0034	10.0	805	2,503,307
15 Sep	1,606	3,267	0.0072	20.1	565	1,846,432	0.0051	14.5	670	2,189,469	0.0046	13.2	697	2,277,038	0.0034	10.1	763	2,492,182	0.0033	9.8	768	2,510,369
1 Oct	1,702	3,464	0.0071	19.8	504	1,745,269	0.0050	14.3	618	2,141,587	0.0045	13.0	648	2,244,858	0.0034	9.9	722	2,501,934	0.0033	9.7	729	2,523,876

Table 11

Fecundity, mortality, cohort size, and potential egg deposition of maiden 2SW Atlantic salmon returning to the Miramichi River at various times. Fecundity (1.636 eggs g^{-1}) is from Randall 1989. Weights and mortalities for salmon entering rivers after 1 July are from Scenario 23, Table 7 (logistic growth, return at 2SW on 1 Oct, 20% mortality upon river exit, allometric mortality using Lorenzen's (1996) b (-3.05), with Mu d^{-1} adjusted to yield given sea survivals).

Date	Salmon fast after 1 Jul					
	Wt. (g)	Fecundity	Mortality 1% month^{-1}			
			Instantaneous daily mortality	Monthly mort. (%)	Cohort size	Potential egg deposition
Mortality eqn.: $M_u\ d^{-1}$			NA			
Mortality eqn.: b			NA			
1 Jul	2,820	4,613	0.0003	1.0	1,000	4,613,238
15 Jul	2,820	4,613	0.0003	1.0	995	4,592,347
1 Aug	2,820	4,613	0.0003	1.0	990	4,567,106
15 Aug	2,820	4,613	0.0003	1.0	986	4,546,423
1 Sep	2,820	4,613	0.0003	1.0	980	4,521,435
15 Sep	2,820	4,613	0.0003	1.0	976	4,500,959
1 Oct	2,820	4,613	0.0003	1.0	971	4,477,672

Date			Salmon remain at sea and feed after 1 Jul																			
	Wt. (g)	Fecundity	Sea survival 1%				Sea survival 3.7%				Sea survival 5%				Sea survival 10%				Sea survival 1.90%			
			Instantaneous daily mortality	Monthly mort. (%)	Cohort size	Potential egg deposition	Instantaneous daily mortality	Monthly mort. (%)	Cohort size	Potential egg deposition	Instantaneous daily mortality	Monthly mort. (%)	Cohort size	Potential egg deposition	Instantaneous daily mortality	Monthly mort. (%)	Cohort size	Potential egg deposition	Instantaneous daily mortality	Monthly mort. (%)	Cohort size	Potential egg deposition
Mortality eqn.: $M_u\ d^{-1}$			0.06865				0.04815				0.04343				0.02807				0.05861			
Mortality eqn.: b			-0.305				-0.305				-0.305				-0.305				-0.305			
1 Jul	2,820	4,613	0.0061	17.2	1,000	4,613,238	0.0043	12.4	1,000	4,613,238	0.0039	11.3	1,000	4,613,238	0.0029	8.6	1,000	4,613,238	0.0052	14.9	1,000	4,613,238
15 Jul	2,969	4,857	0.0060	16.9	919	4,462,975	0.0042	12.2	942	4,577,131	0.0038	11.1	948	4,603,814	0.0028	8.4	961	4,665,834	0.0051	14.7	930	4,518,516
1 Aug	3,182	5,206	0.0059	16.6	831	4,324,458	0.0041	12.0	878	4,570,656	0.0037	10.9	889	4,629,272	0.0028	8.3	916	4,767,088	0.0050	14.4	854	4,443,316
15 Aug	3,387	5,541	0.0058	16.3	766	4,243,226	0.0040	11.8	829	4,595,139	0.0036	10.7	845	4,680,175	0.0027	8.1	881	4,881,971	0.0049	14.1	796	4,412,053
1 Sep	3,675	6,012	0.0056	16.0	695	4,179,860	0.0039	11.5	775	4,659,125	0.0036	10.4	795	4,776,984	0.0027	7.9	842	5,059,772	0.0048	13.8	733	4,408,056
15 Sep	3,947	6,457	0.0055	15.7	643	4,152,850	0.0039	11.3	734	4,737,811	0.0035	10.2	756	4,883,699	0.0026	7.8	811	5,236,865	0.0047	13.5	686	4,429,676
1 Oct	4,297	7,029	0.0054	15.3	590	4,144,891	0.0038	11.0	690	4,852,925	0.0034	10.0	716	5,032,293	0.0025	7.6	778	5,470,834	0.0046	13.2	637	4,477,672

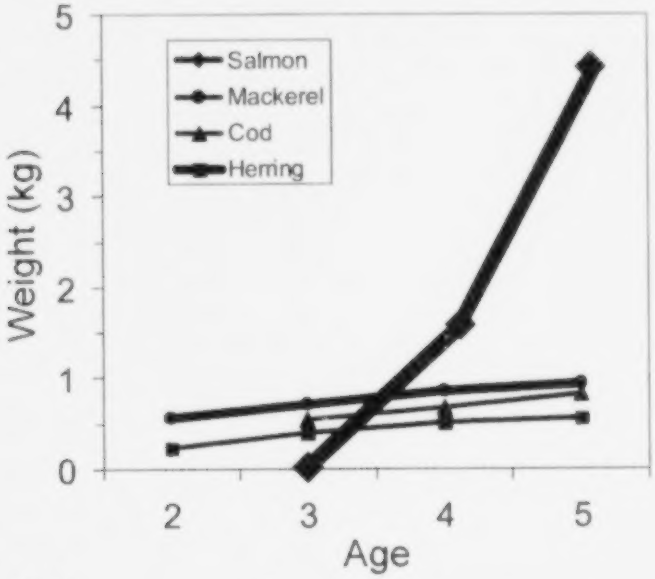

Fig. 1
Growth of four fish species in the northwest Atlantic. Salmon weights are from 23 May for sea ages 0, 1, and 2, assuming logistic growth, and a smolt age of 3 years. Mackerel and herring weights are from Scott and Scott 1988.

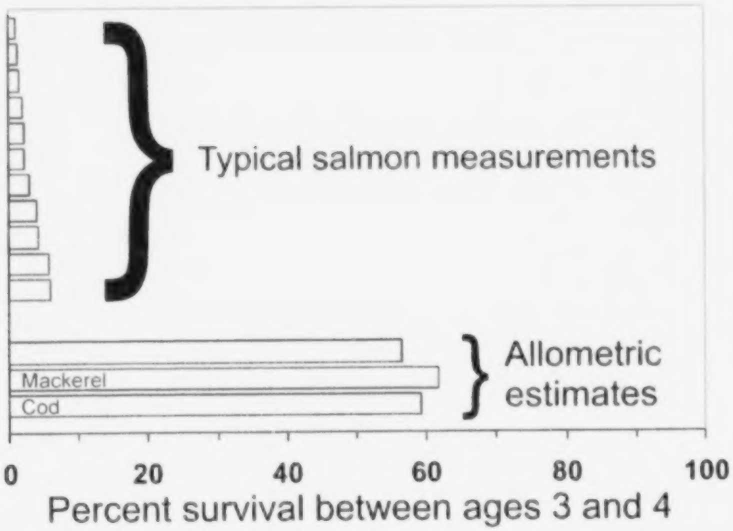

Fig. 2
Percent survival between ages 3 and 4 of Atlantic salmon and other fish of the Northwest Atlantic. It is assumed that Atlantic salmon enter the sea at age 3. Allometric estimates are based on weight, using Lorenzen's (1996) formula.

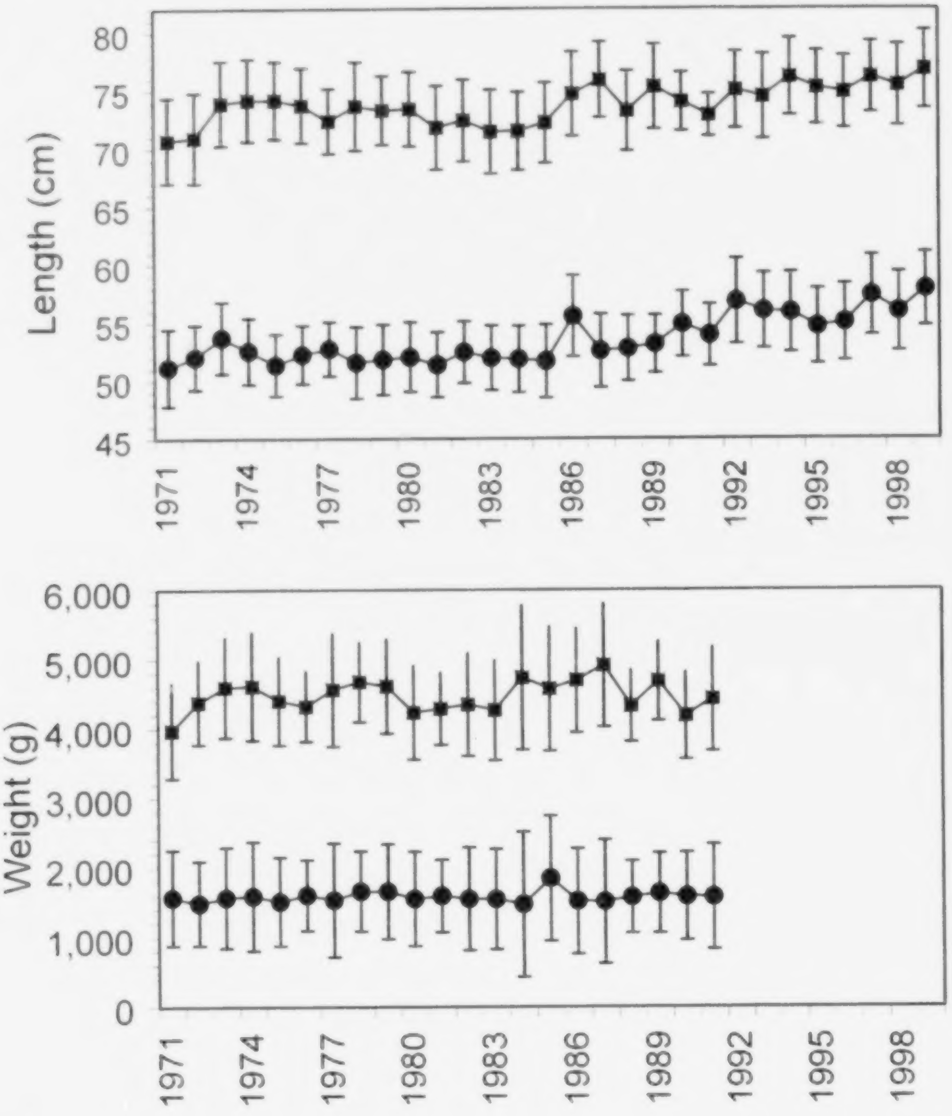

Fig. 3
Mean (± SD) lengths and weights of maiden 1SW (circles) and 2SW (squares) salmon captured in assessment traps in the Miramichi River. Weight data are unavailable after 1991.

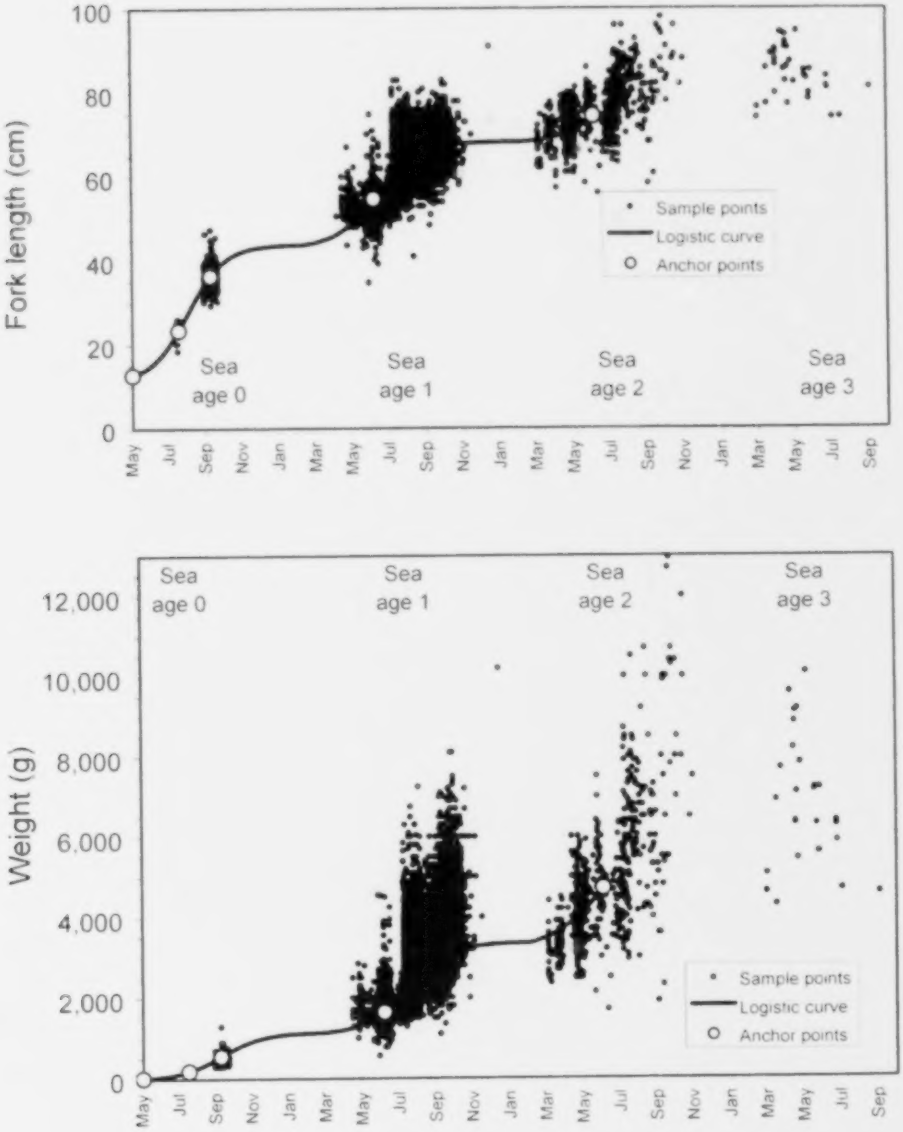

Fig. 4

Lengths and weights of Atlantic salmon sampled at sea. The logistic curves are fitted to anchor points from smolt sampling in the Miramichi River, from post-smolts captured by gannets on Funk Island in August, from post-smolts taken in research cruises in the Labrador Sea in September-October, and from 1SW and 2SW maiden salmon returning to the Miramichi River between 24 June and 7 July. Dots in sea age 0 are from the above-noted studies. Dots in sea ages 1-3 are from the Newfoundland marine sampling program. Miramichi data are from G. Chaput. Funk Island data are from Montevecchi et al. 2002, and Newfoundland and Labrador sampling data are from D.G. Reddin (Cairns and Reddin 2000).

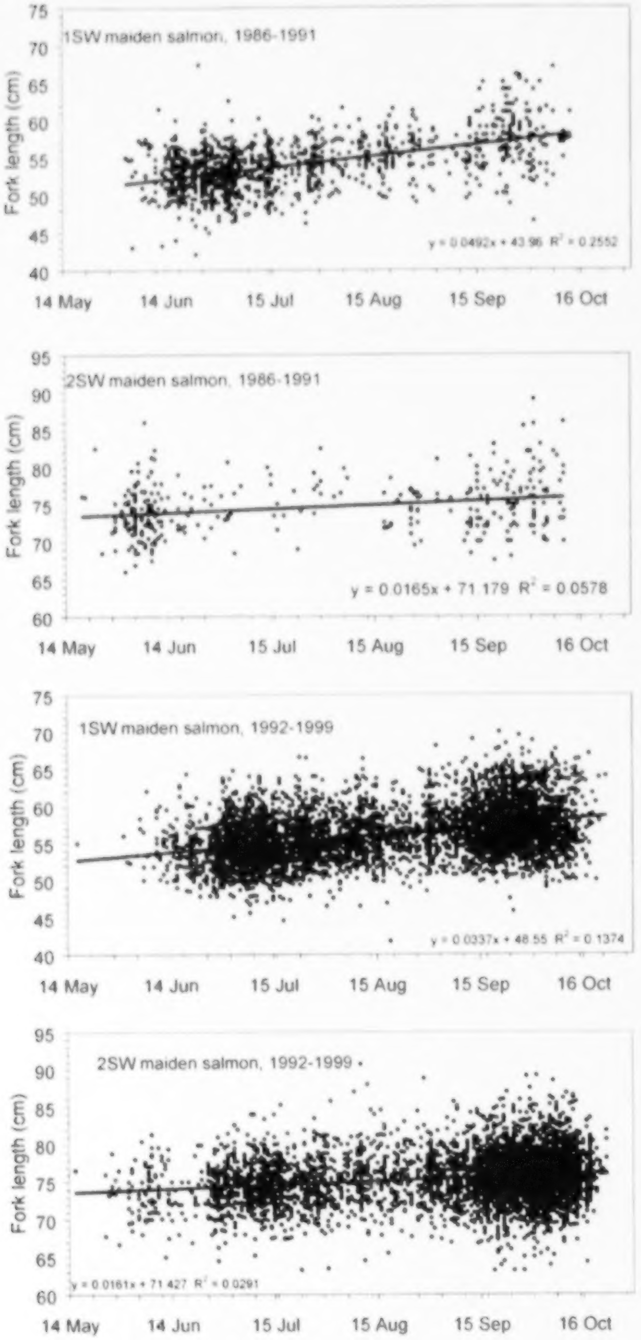

Fig. 5
Fork lengths of 1SW and 2SW maiden Atlantic salmon vs. date of capture in assessment traps in the lower Miramichi River, 1986-1999. Data from G. Chaput.

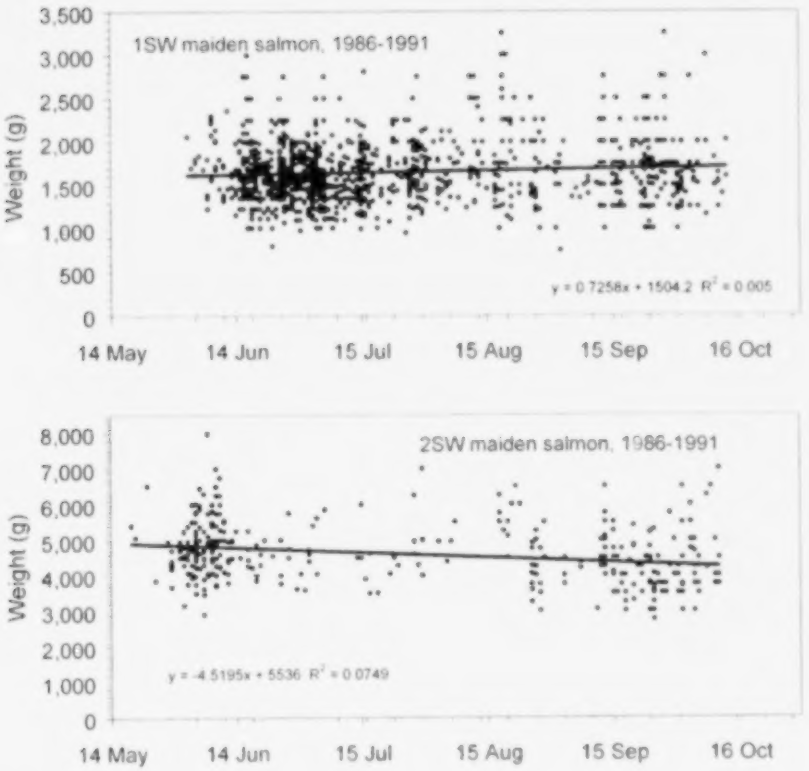

Fig. 6

Weights of 1SW and 2SW maiden Atlantic salmon vs. date of capture at the Millbank trap, Miramichi River, 1986-1991. Data from G. Chaput.

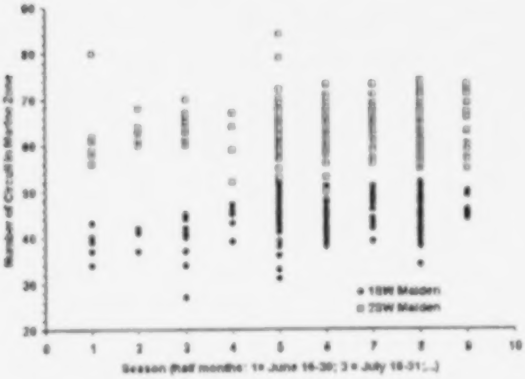

Fig. 7.
Number of marine-zone circuli on scales sampled from 1SW and 2SW maiden salmon captured in the upper estuary trapnet in the Margaree River. Figure provided by G. Chaput (DFO).

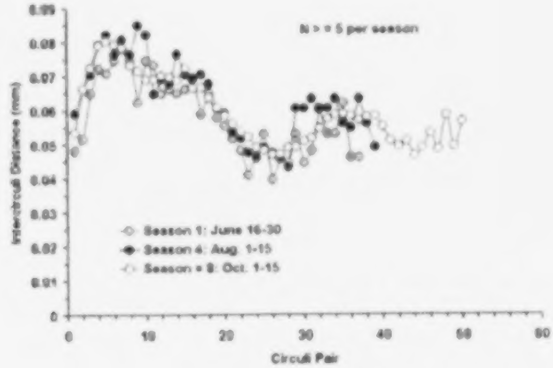

Fig. 8.
Intercirculi distance (mean when sample size > 4 fish) measured on scales of 1SW salmon captured in the Margaree River from June to October. Figure provided by G. Chaput (DFO).

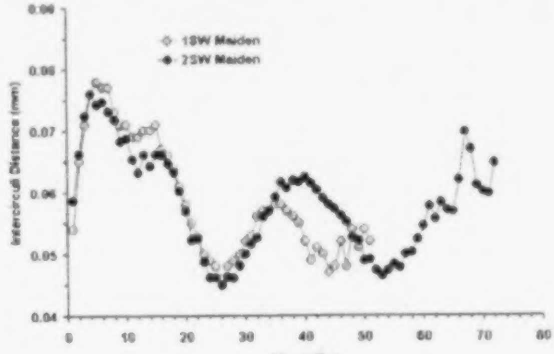

Fig. 9.
Intercirculi distance (mean when sample size > 4 fish) measured on scales of 1SW and 2SW salmon captured in the Margaree River. Samples are from all seasons. Figure provided by G. Chaput (DFO).

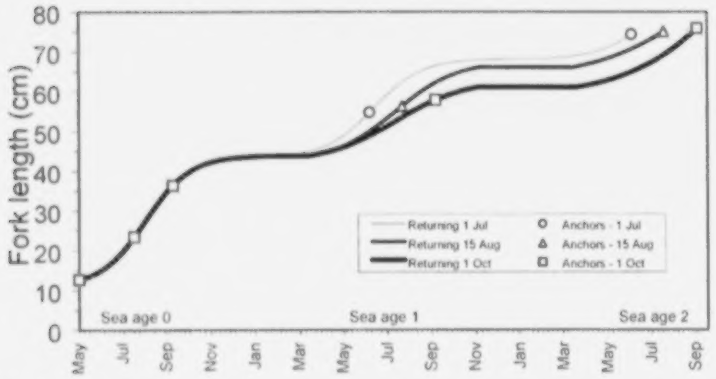

Fig. 10
Growth in length of Atlantic salmon, fitted to logistic equations, for salmon returning to the Miramichi on 1 July, 15 August, and 1 October

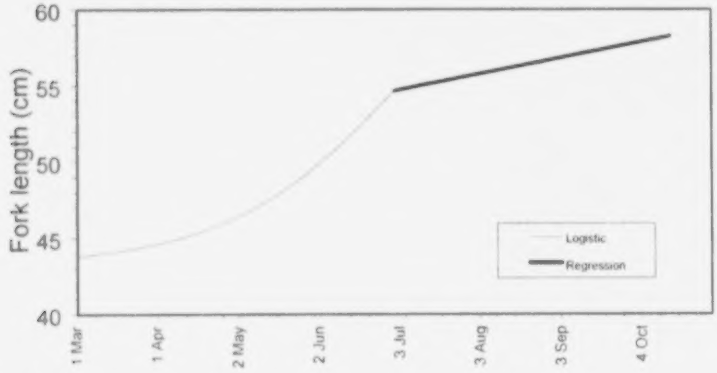

Fig. 11
Growth in length of 1SW Atlantic salmon during the summer of river return. The logistic curve is fitted to logistic equations for salmon returning to the Miramichi on 1 July. The regression line is from lengths of maiden 1SW salmon returning to the Miramichi in 1992-1999.

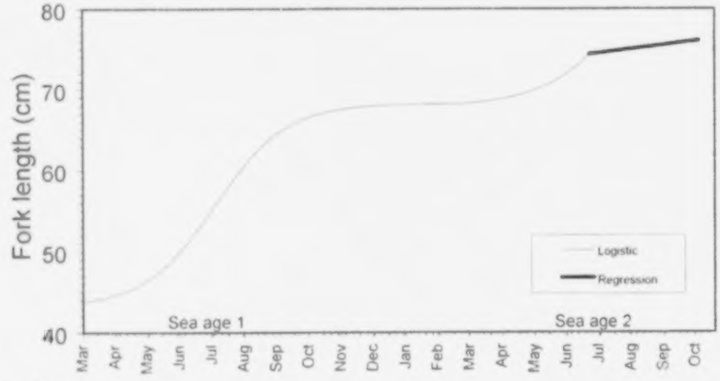

Fig. 12
Growth in length of 2SW Atlantic salmon during their second and third sea summers. The logistic curve is fitted to logistic equations for salmon returning to the Miramichi on 1 July. The regression line is from lengths of maiden 2SW salmon returning to the Miramichi in 1992-1999.

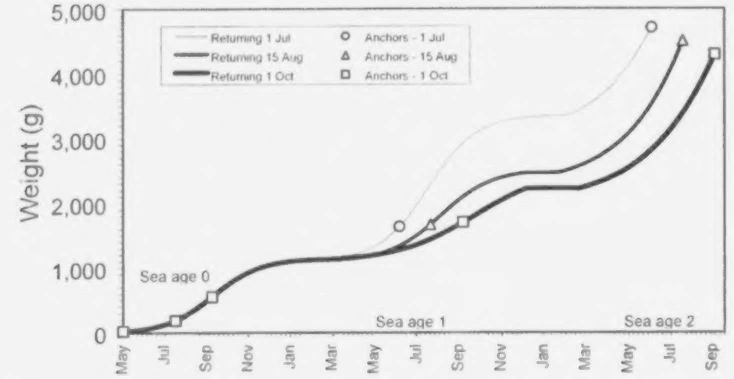

Fig. 13
Growth in weight of Atlantic salmon, fitted to logistic equations, for salmon returning to the Miramichi on 1 July, 15 August, and 1 October.

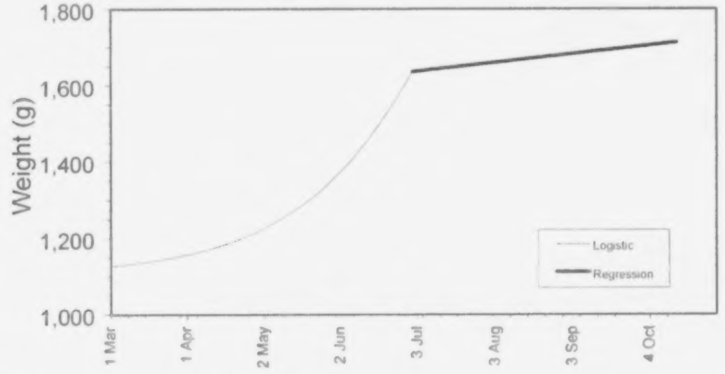

Fig. 14
Growth in weight of 1SW Atlantic salmon during the summer of river return. The logistic curve is fitted to logistic equations for salmon returning to the Miramichi on 1 July. The regression line is from weights of maiden 1SW salmon returning to the Miramichi in 1986-1991.

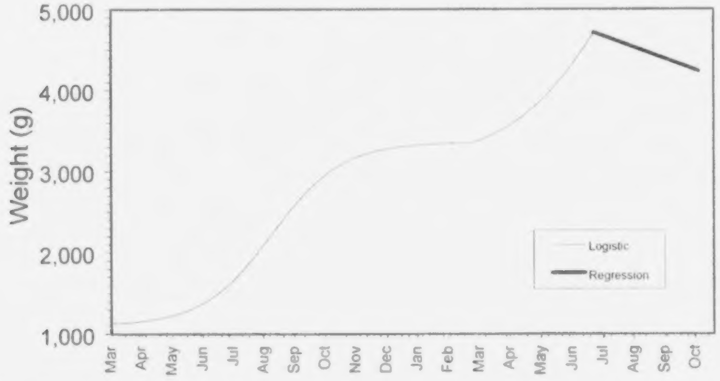

Fig. 15
Change in weight of 2SW Atlantic salmon during their second and third sea summers. The logistic curve is fitted to logistic equations for salmon returning to the Miramichi on 1 July. The regression line is from weights of maiden 2SW salmon returning to the Miramichi in 1986-1991

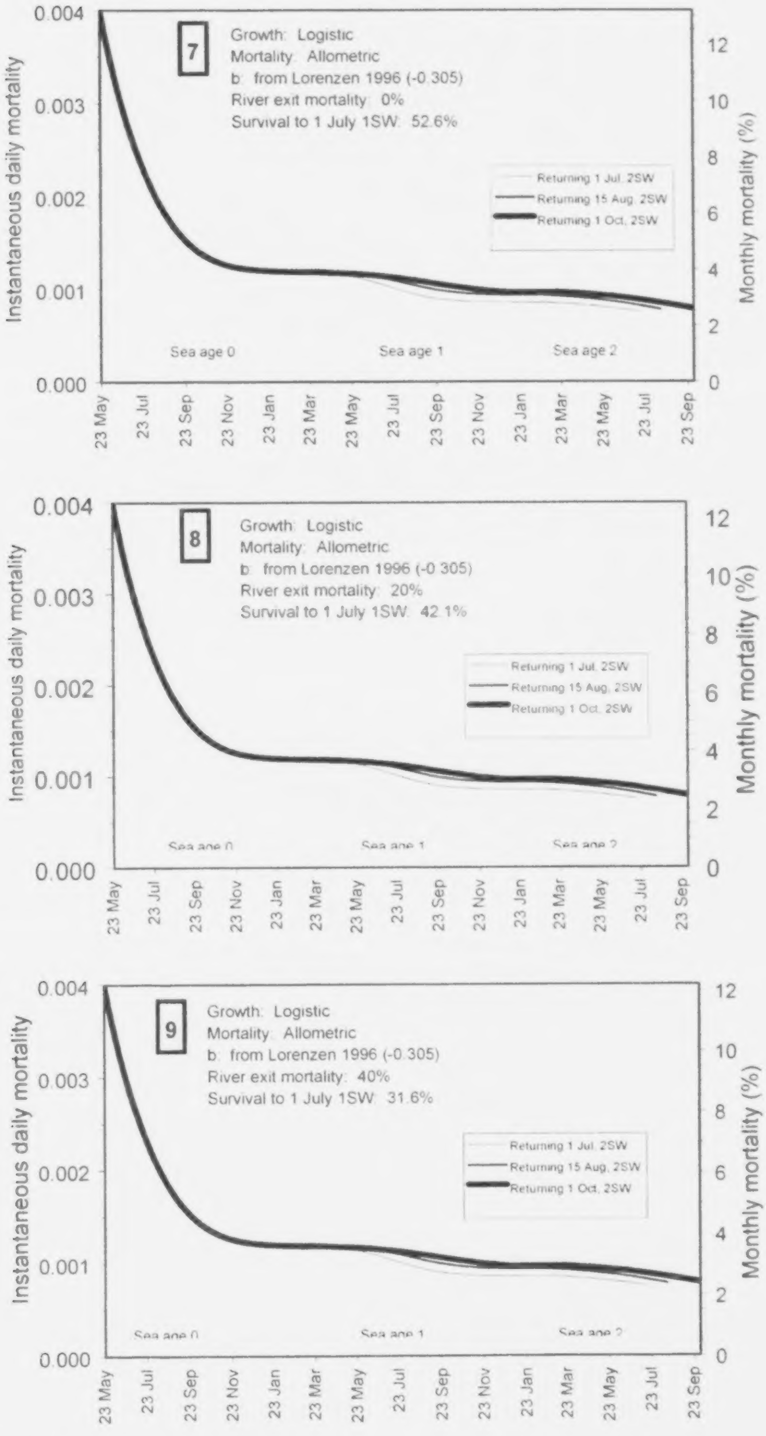

Fig. 16
Marine mortality of Atlantic salmon estimated from Lorenzen's (1996) equation for mortality of ocean fishes. Weights are from logistic equations. Numbers in boxes are scenario numbers.

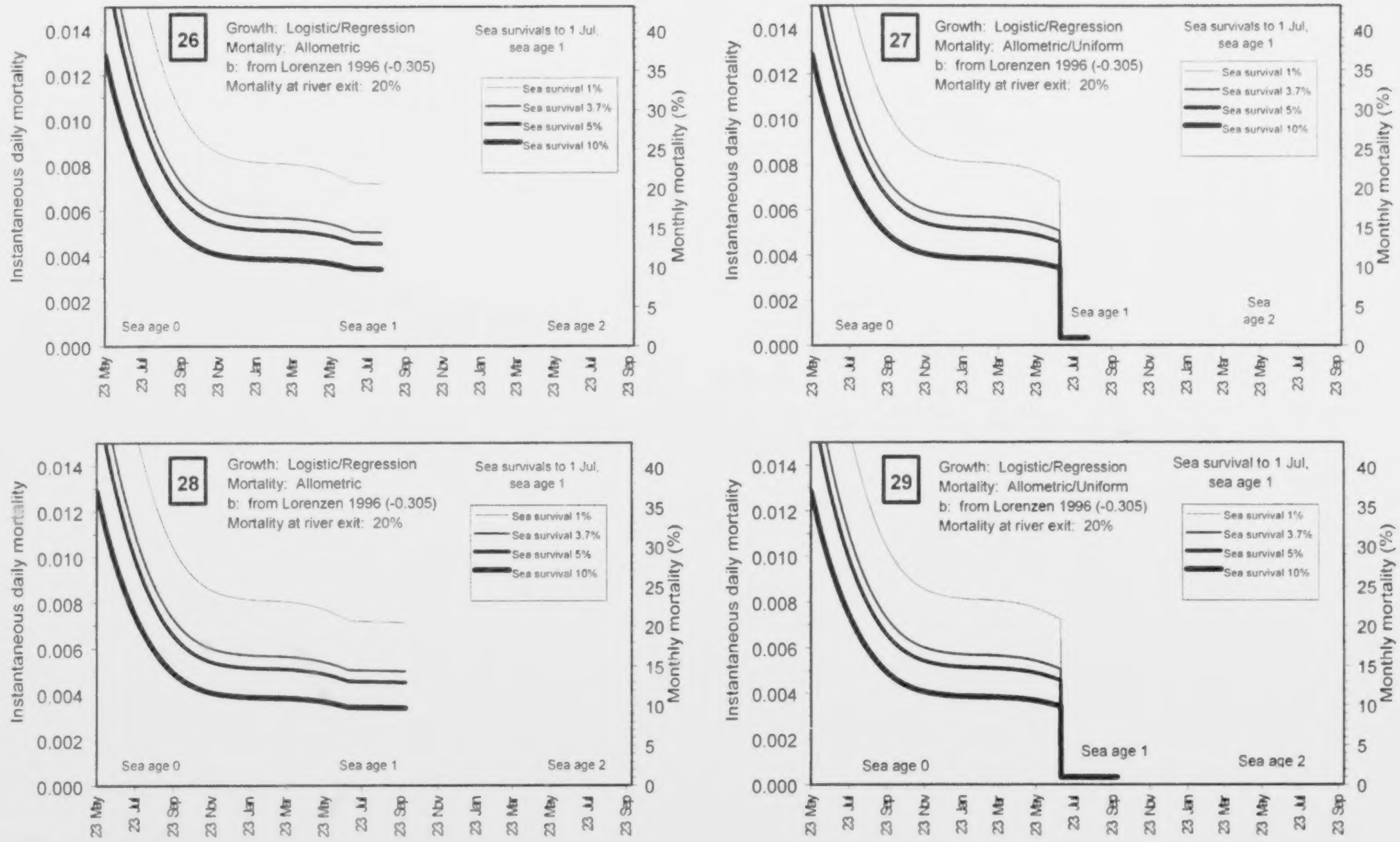

Fig. 17
Marine mortalities of Atlantic salmon, assuming river return on 15 Aug or 1 Oct at sea age 1. Growth after 1 July is calculated by a regression formula; otherwise growth is logistic. Numbers in boxes are scenario numbers

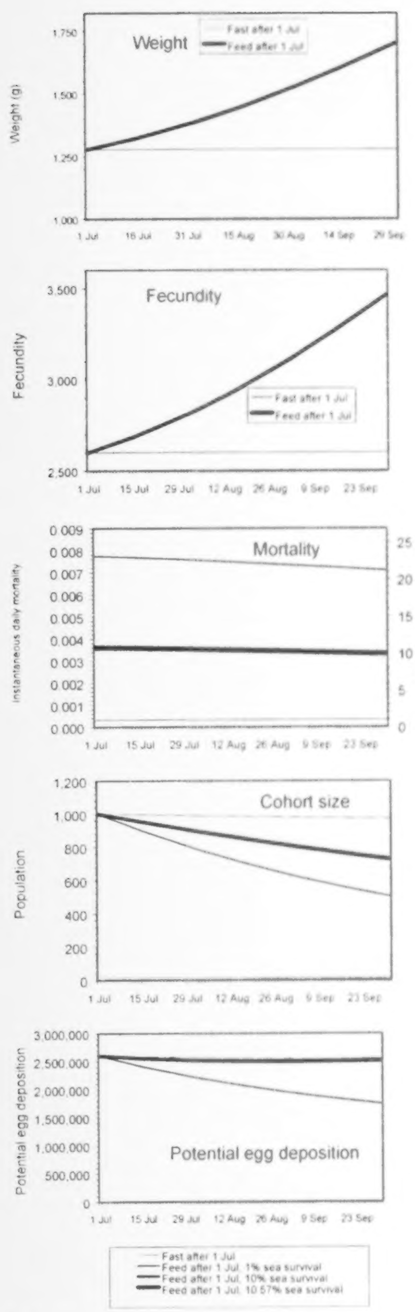

Fig.18
Weights, fecundities, mortalities, cohort sizes, and potential egg deposition of maiden 1SW Atlantic salmon returning to fresh water, under various scenarios. See Table 1 for assumptions.

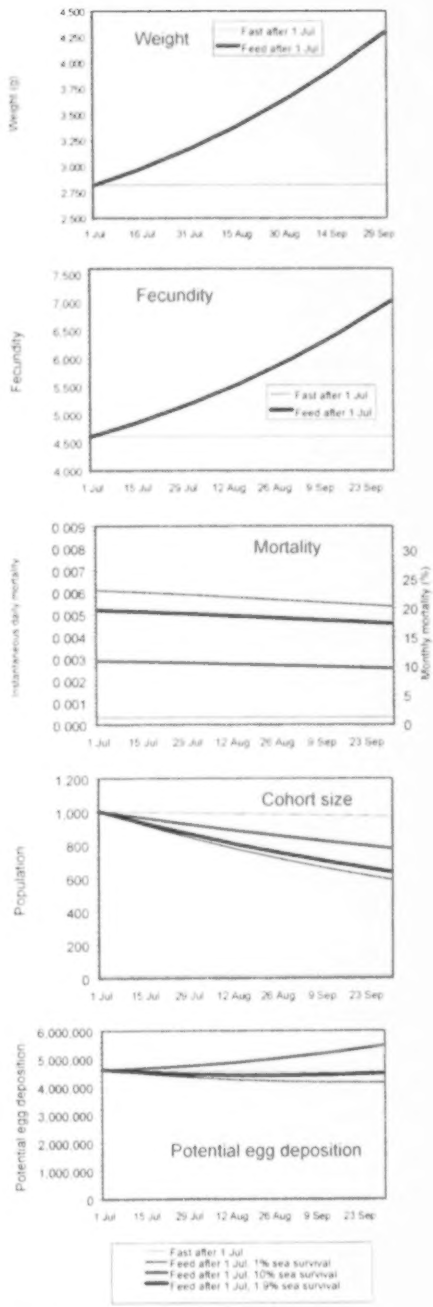

Fig. 19
Weights, fecundities, mortalities, cohort sizes, and potential egg deposition of maiden 2SW Atlantic salmon returning to fresh water, under various scenarios. See Table 2 for assumptions.

13

ESTIMATION OF MARINE EXPLOITATION RATES ON ATLANTIC SALMON (*Salmo salar L.*) STOCKS IN NEWFOUNDLAND, CANADA

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EXTENDED ABSTRACT

Marine exploitation rates were estimated for nine Newfoundland Atlantic salmon (*Salmo salar* L.) populations, separately for small and large salmon size components (Dempson et al. 2001). Estimates were derived using counts of salmon returning to fish counting facilities rather than from tagging studies and thus adjustments were not required to account for tag loss, handling or tagging mortality, or tag reporting rates. It is a variation of an approach used by Scarnecchia et al. (1989) to determine the harvest rate required to account for a change in the grilse to two-sea-winter (2SW) salmon ratio in various Icelandic rivers following the expansion of the commercial salmon fishery at West Greenland. Given the closure of the Newfoundland commercial salmon fishery, the approach proceeded by considering the average marine exploitation rate (*ME*) required to account for the difference in average returns between the pre-moratorium and moratorium period for each river, separately for small and large-sized Atlantic salmon:

$$ME = \frac{\overline{Rm} - \overline{Rpm}}{\overline{Rm}} \text{ x } 100$$

where,

$\overline{Rm}$ = average total returns during the moratorium (1992-1996), and

$\overline{Rpm}$ = average total returns prior to the moratorium (1984-1991)

For all stocks combined, the overall marine exploitation rate during the period 1984-1991 averaged 45.3% (29.6-57.1%) on small salmon and 74.2% (57.7-83.7%) on large salmon. These estimates are considered minimum values. Results are discussed in relation to previous estimates derived from tagging, and highlight the importance of accounting for marine exploitation when examining trends in salmon survival and return data even when commercial fisheries have been closed.

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Scarnecchia, D.L., A. Isaksson and S.E. White. 1989. Oceanic and riverine influences on variations in yield among Icelandic stocks of Atlantic salmon. Transaction of the American Fisheries Society 118:482-494.

EVALUATION OF AN ALTERNATIVE STRATEGY TO ENHANCE ATLANTIC SALMON (*Salmo salar* L.) POPULATIONS: CAGE REARING WILD SMOLTS FROM CONNE RIVER, NEWFOUNDLAND

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EXTENDED ABSTRACT (Dempson et al. 1999)

Five thousand wild Atlantic salmon (*Salmo salar* L.) smolts from Conne River, Newfoundland, were captured during their downstream migration in May 1995, and transferred to an estuarine aquaculture rearing site at Roti Bay, 23 km away. Survival was monitored throughout the experiment. The greatest mortality occurred in July, approximately six-to-eight weeks following transfer after which mortality stablized over the remainder of the time smolts were held. It is unknown, however, whether the timing of smolt mortality in natural situations occurs at similar intervals following the migration of smolts to sea. Overall, survival of smolts to one-sea-winter salmon was 18.5%, over four times higher than the average survival of wild salmon to Conne River during the past six years.

Growth of smolts was monitored at monthly intervals until November 1995, with additional sampling in the spring and early summer of 1996. Survivors were split into two groups and released directly into the Bay d'Espoir fiord; one group was released 27-28 June, 1996, at a site approximately 7 km from the mouth of Conne River. The second group was retained at Roti Bay and released 23 July, 1996. Lotek radio transmitter tags were used in evaluating the success of the experiment by tracking migration timing and subsequent distribution of cage released salmon throughout the Conne River system. Approximately 80% returned to Conne River, 20% strayed to other streams. Less than 50% of the surviving fish were later accounted for in local Bay d'Espoir rivers. Results are discussed in relation to the utility of this technique to enhance salmon populations.

References

Dempson, J.B., V.A. Pepper, G. Furey, M. Bloom, T. Nicholls, and G. Hoskins. 1999. Evaluation of an alternative strategy to enhance salmon populations: cage rearing wild smolts from Conne River, Newfoundland. ICES J. Mar. Sci. 56: 422-432.

14

SIMPLE MODELS TO TEST FOR FLOW-DEPENDENT MORTALITY OF RETURNING ATLANTIC SALMON (*Salmo salar* L.)

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INTRODUCTION

The choice of backward-running (run-reconstruction) models rather than forward-running (life-history) models to estimate pre-fishery abundance of North Atlantic salmon (*Salmo salar* L.) (Rago et al. 1993; Potter et al. 1998) has been strongly influenced by the belief (or assumption) that natural mortality is quite high and variable in the post-smolt phase but much lower and more stable after the first sea year. Based upon the inverse-weight hypothesis (Doubleday et al. 1979), ICES has previously employed a value of 0.01 per month for the rate of natural mortality of salmon after the first sea winter (e.g. ICES 2000), although ICES (2002) has now modified the value used to 0.03. Thus mortality is not only assumed to be constant for adult salmon in the sea but is also assumed not to vary significantly between years for this part of the life cycle. It is well known, however, that low river flows delay the upstream migration of salmon, resulting in reduced runs, at least while the low flows persist (e.g. Potter, 1988). If fish that are delayed are more likely to die than those moving upstream into the comparative safety of freshwater, then the overall natural mortality on the stock may be higher in years with low flows than in years with high flows.

In this paper we explore this question by examining the effect of variation in daily flows within a year, using a simple model in which flow variation is represented as the number of days above or below some critical value. We refer to these as low flow and high flow periods respectively. The numbers of salmon migrating upstream might be expected to be lower than average during periods of low flows. Further, they may be greater during high flows following a low flow period if salmon simply queue for the next high flow, and the number may increase with the length of the low sequence. Also, the numbers running at the beginning of a high flow might be expected to be higher than average if the majority of the salmon in a queue start to run immediately.

We also present a second simple model to test whether salmon are "lost" to a river because of low summer flows. The model consists of two parts: the first uses the relationship between the annual summer run of salmon and annual summer flow to estimate the number of salmon lost during the summer. The second part then tests to see if all or only a part of these "lost" salmon enter the river during the autumn.

Both these models have been tested on the salmon counts recorded on the Fisheries Research Services salmon counter on the River North Esk, Scotland during the period 1988-97. Salmon enter this river throughout the year, but, as on most rivers, different sea-age groups return during different periods.

However, the counter is unable to discriminate between fish of different ages, so no account has been taken of age in the analyses.

MODEL 1 - EFFECT OF HIGH OR LOW DAILY FLOWS

Figure 1 shows the time series of daily salmon counts and flows in the River North Esk for the 10 years 1988-97. There is little evidence of any direct relationship between counts and flow, which is not unexpected due to the seasonal nature of salmon runs. We therefore fit a model where counts are assumed to follow a negative binomial distribution and are described by a generalised linear model with a log link and four variables. These are Year; Month; Day number (in the current sequence of Low or High flows); and Number of days (in the previous sequence of Low or High flows).

High and Low are respectively defined as flows above or below some threshold, which is estimated from the data by minimising the residual sum of squares. The conversion flow to High/Low is shown in Figure 2. In the upper figure, daily flows are shown plotted against day number together with a threshold of 5 m^3s^{-1}. In the lower figure, flows are converted to the day number in a sequence of flows above (Hi = +ve) or below (Lo = -ve) the threshold. Hence the flow on a particular day can be characterised by the length of the previous sequence, whether this was High or Low, and the cumulative duration of a flow sequence on that day.

To avoid having to assume any parametric form (e.g. linear or quadratic) for the effect of Day number or Number of days, they were converted to factor levels, as follows:

Factor level	Day range	Span
1	1	1 day
2	2-3	2 days
3	4-7	4 days
4	8-14	1 week
5	15-30	2 weeks
6	31-90	2 months
7	90-180	3 months
8	181+	6 months+

Hence there is a separate parameter for each factor level. Then the effects of Year, Month, Day Number and Number of days were tested using a multi-factorial generalised linear model, with fish-counts assumed to follow a Poisson distribution. Model terms were tested assuming that the decrease in deviance from adding a model term follows a chi-squared distribution. Year and Month were added to the model first, followed by Day Number and Number of days. However, because of the lack of balance in the data, within each pair, each factor was fitted both unadjusted and adjusted for the other model terms. Further evaluation of the effect of Number of Days tested whether the mean count was in proportion to the length of the preceding sequence of High or Low flows.

Application of model 1

The estimated threshold flow for the River North Esk data set was an average daily flow of 5 m^3s^{-1} as shown in Figure 2. Figure 3 shows large differences in mean counts both between and within Years, reflected in the analysis of deviance table (Table 1). Both Day Number and Number of days are statistically significant (Table 1). Their effects are shown in Figure 4, which shows the means of the unadjusted and adjusted deviance residuals plotted against each factor when it is excluded from the model. The strongest effect is for Day Number. Counts tend to be below average during Low flows, and above average in the first days of High flows.

Table 1 also shows a significant interaction between Day Number and Number of days, and also indicate that counts do not vary in a simple way with the length of the previous sequence. This is revealed in more detail in Figure 5. This shows the deviance residuals plotted against Number of days separately for each of the first three levels of Day Number for both High and Low sequences.

MODEL 2. - EFFECT OF WET OR DRY YEARS

This model tests whether salmon are "lost" to a river as a result of low summer flows. Step 1 uses the relationship between the annual summer run of salmon and annual summer flow to estimate the number of salmon delayed during the summer, and Step 2 then tests to see if all or only a part of these delayed salmon are recovered during the autumn.

Step 1: Summer

Let S_i and f_i be the size of the salmon run and the river flow during the summer. In year i we assume that S_i decreases from a fixed maximum mean level $S_{\max}$ as f_i approaches a critical flow c, i.e.

$$S_i = S_{\max}\frac{f_i - c}{f_i} + \varepsilon_i$$

where c is a constant and ε_i is a noise term. Then the expected loss in year i can be estimated as

$$\hat{L}_i = \hat{S}_{\max} - \hat{S}_{\max}\frac{f_i - c}{f_i} = \hat{S}_{\max}\frac{c}{f_i}.$$

Step 2: Autumn

Let W_i be the autumn run of salmon in year i. We assume that this is increased from a fixed minimum mean level $W_{\min}$ by a proportion of the estimated number of fish lost during the summer. i.e.

$$W_i = W_{\min} + k\hat{L}_i + \delta_i \quad 0 <= k <= 1$$

where k=1 implies that all of the lost salmon are recovered, and δ_i is a noise term.

Application of model 2

We applied this model to ten years of salmon counts collected on the River North Esk. The model was fitted by least squares under the assumption that the noise terms are independent and normally distributed with constant variance.

Figure 6 shows the monthly mean summer and autumn flows and salmon runs plotted against year. Summer is defined as June-August; autumn as September-November. Figure 7(left panel) shows the model for summer run as a function of summer flow. The fitted model for this step was

$$S_i = 69.1\frac{f_i - 2.7}{f_i} + \varepsilon_i .$$

The autumn run as a function of the estimated summer losses (Step 2) is shown in Figure 7. The solid line corresponds to the overall best fit and the dashed line corresponds to the model constrained to have k = 1. The two fitted models are:

$$W_i = 35.0 + 0.787L_i + \delta_i$$

and, with k = 1,

$$W_i = 28.7 + L_i + \delta_i$$

A test of H_0: k = 1 versus H_1: k < 1 gave a p-value of 0.36; i.e. there is no evidence that salmon "lost" from the river in years of low summer flow are not recovered during the autumn run.

DISCUSSION

The results from Model 1 show that mean salmon counts for the River Esk changed between periods of High and Low flows. From Figure 4, there is a suggestion that counts are lower during Low flows, and higher in the days immediately following a switch to High flows. However, there is no clear evidence of any simple effect of the duration of the preceding sequence on the numbers moving upstream. It is therefore possible that once fish are delayed by more than a few days they are less likely to be stimulated to move upstream on increased flows. This has been observed in some tracking studies (Potter, 1988).

Model 2 appears to fit reasonably well, but the recovery factor, k, does not show a significant deviation from unity. Thus it does not support the hypothesis that fish delayed during the summer months are 'lost'. However, the high variability in the autumn run as a function of summer losses, together with the small number of years, implies that the model has poor power to detect any shift in k from unity. It would therefore be useful to update this data set or apply the model to other data sets, preferably with more data points.

We have assumed that there are no trends in the underlying means of either summer or autumn salmon runs, although the model could be extended to allow for such a trend. However, there were no suggestions of trends in Figure 1b, and given the small number of years, it seemed inappropriate to apply any correction. There is also a danger that applying a correction could mask a trend in natural mortality caused by a progressive change in environmental regimes. Ideally this should be evaluated for any data sets to which the model is applied.

The results suggest that the potential size of the summer run (S_{max} = 69) is higher than the un-recovered autumn run (W_{min} = 35), and that, on average, about 40% of the observed autumn run consists of salmon delayed during the summer run by low flows. The results here can be compared with those obtained with Model 1, in which periods of High and Low flows were defined relative to an estimated threshold. The data suggested that the mean number of salmon running was reduced during periods of Low flows, with recovery indicated by a higher mean during periods of High flows. However, recovery tended to take place during the days immediately following the switch from Low to High flow. One criticism of this model is that effects may be different in summer and autumn, in that fish may exhibit different responses to flow at different times of year, and this is one aspect that could be studied further.

ACKNOWLEDGEMENT

We are very grateful to Julian MacLean of FRS Scotland for allowing us to use the data from the North Esk salmon counter to test these models. It is with deep regret to members of SALMODEL and his

colleagues at CEFAS and in the wider scientific community that Mike Nicholson died accidentally on June 6, 2003.

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Table 1. Analysis of Deviance.

	df Difference	Deviance Difference	p value
month	11	1359.29	0.0000
month (adjusted for year)	11	1341.86	0.0000
year	9	97.69	0.0000
year (adjusted for month)	9	80.27	0.0000
year x month	99	632.45	0.0000
Day number in sequence	13	458.61	0.0000
Day number in sequence (adjusted)	12	269.28	0.0000
Number of days in previous sequence	13	215.04	0.0000
Number of days in previous sequence (adjusted)	12	25.70	0.0118
Linear no days in previous sequence	1	3.75	0.0529
separate lines	13	31.53	0.0028
Day No x No of days	63	124.21	0.0000
lack of linear fit	61	114.64	0.0000

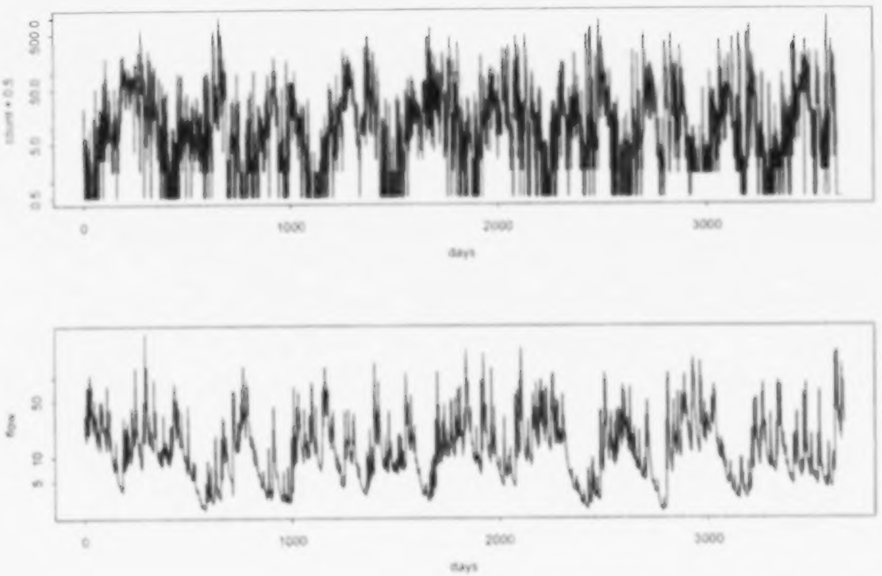

Figure 1 Time series of daily counts (upper panel) and flows (lower panel) for the River North Esk. [Day 1 equals 1st January 1988)

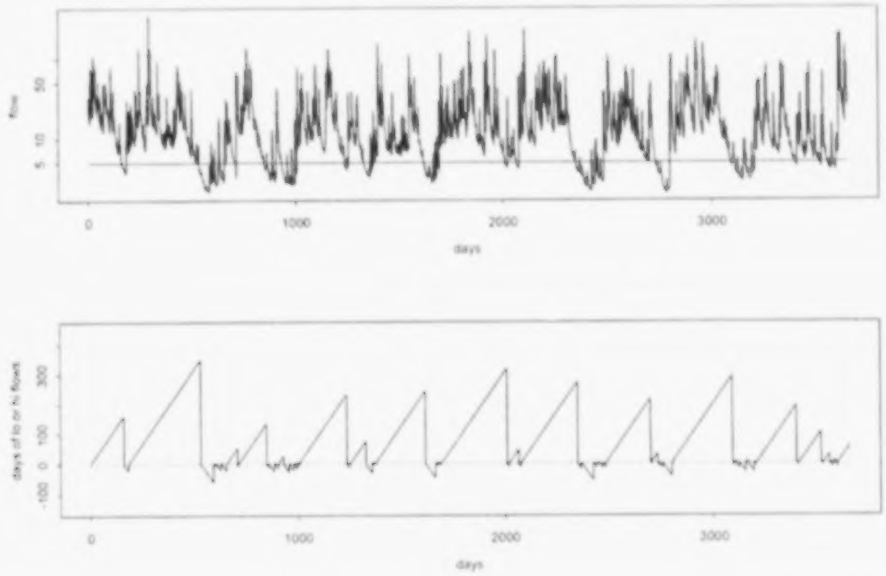

Figure 2. Daily flows for the River North Esk for 1988-1997 (upper panel) and daily flows converted to sequences of Lo (-) and Hi (+) flows relative to threshold level of 5 m^3s^{-1} (lower panel).

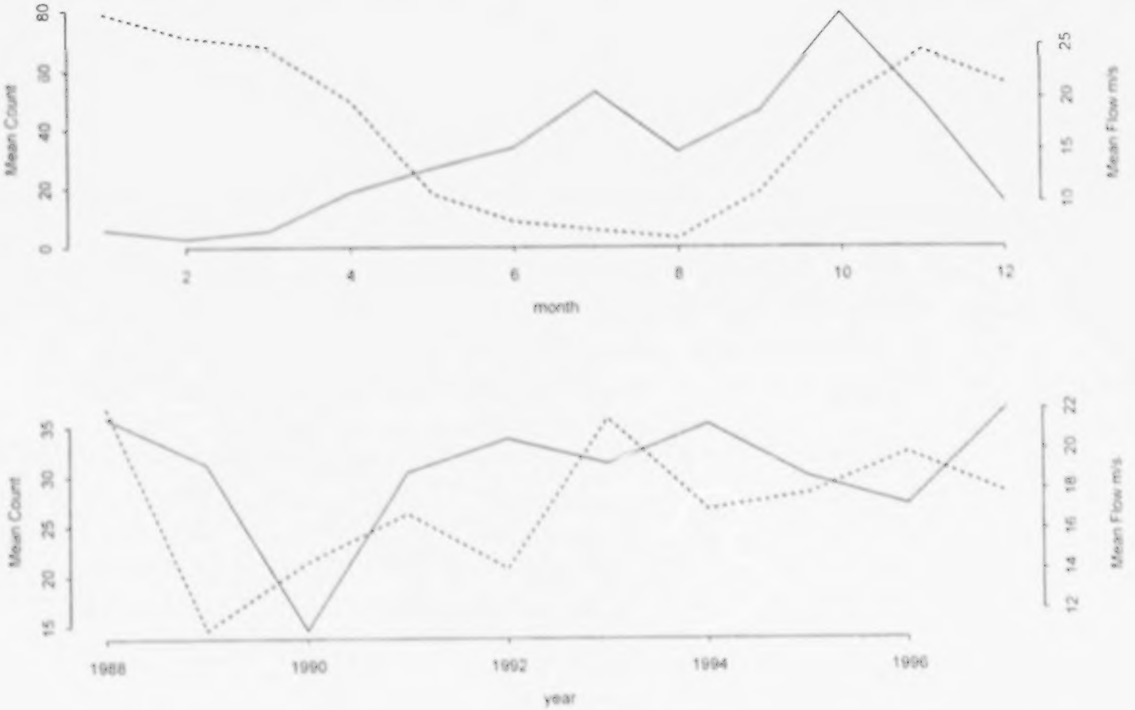

Figure 3. Monthly (upper panel) and yearly (lower panel) means of counts (solid) and flows (dashed).

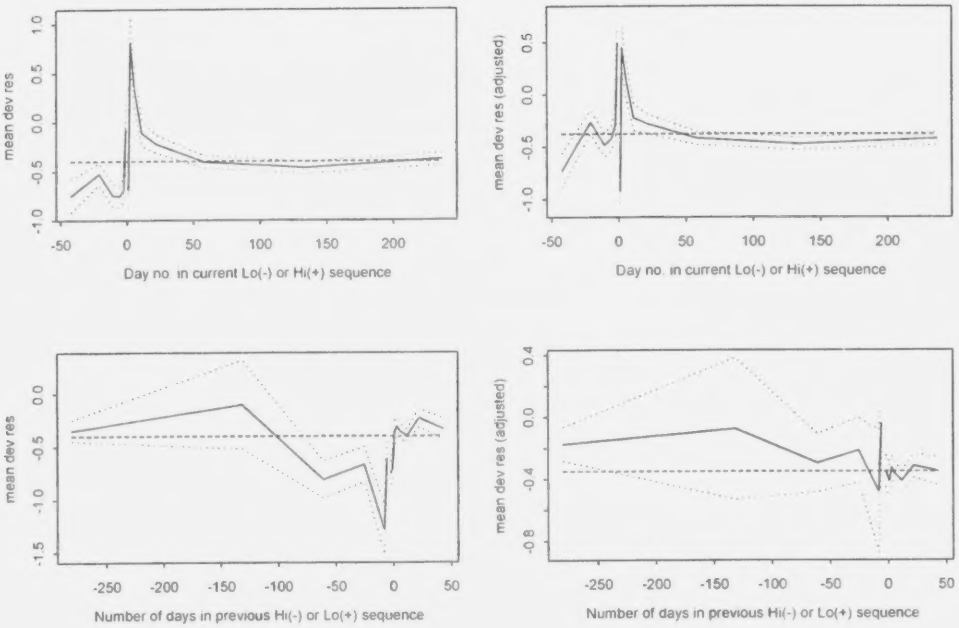

Figure 4. Means of the unadjusted (left panels) and adjusted (right panels) deviance residuals plotted against each factor when it is excluded from the model.

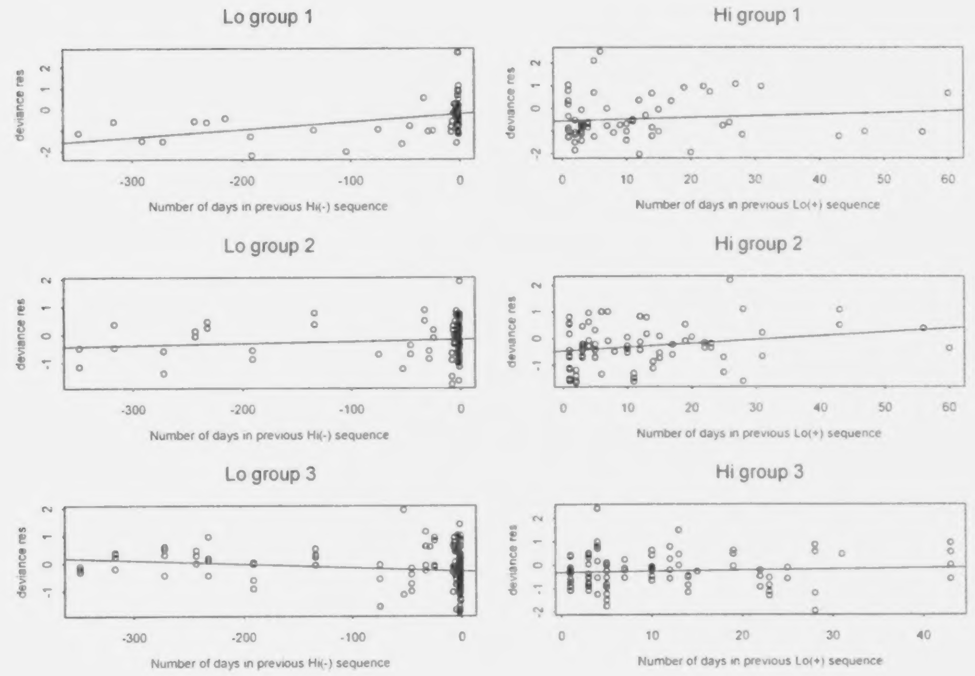

Figure 5. The deviance residuals plotted against Number of days separately for each of the first three levels of Day Number for both High and Low sequences.

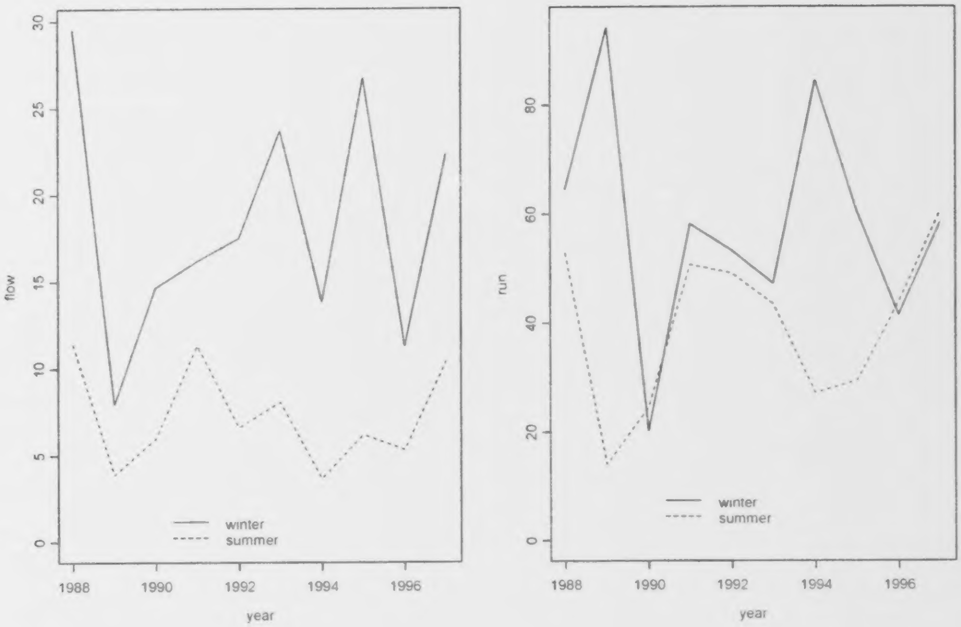

Figure 6. Monthly mean summer (June-August) and autumn (September-November) flows (left panel) and salmon runs (right panel) plotted against year.

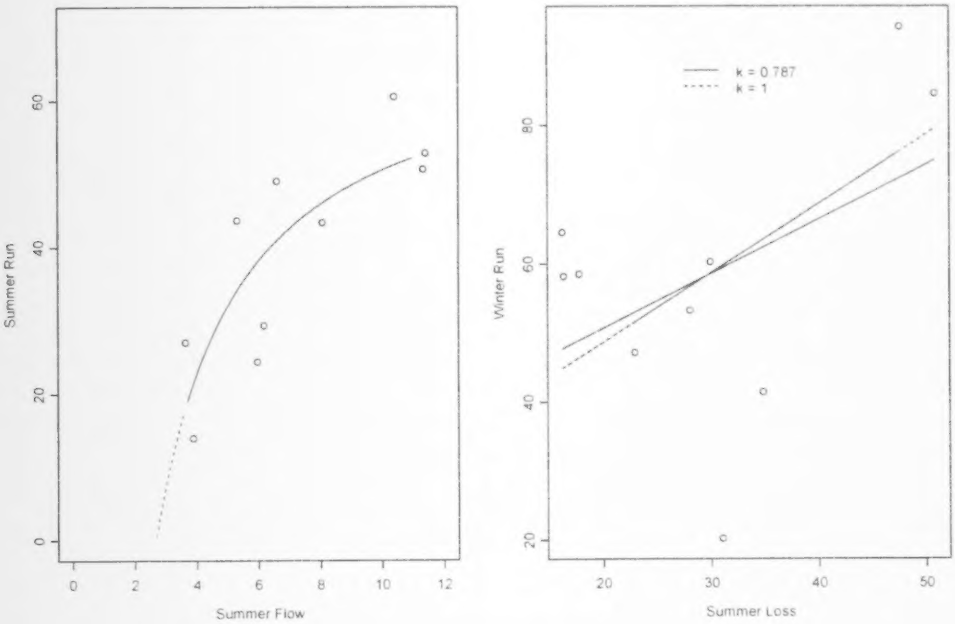

Figure 7. Model for summer run as a function of summer flow (left panel) and autumn run as a function of the estimated summer losses (right panel). The solid line corresponds to the overall best fit, the dashed line corresponds to the model constrained to have k = 1.

APPENDIX 1. LIST OF PARTICIPANTS AT THE ATLANTIC SALMON MORTALITY WORKSHOP, AUGUST 24-26, 2001.

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